ECOLOGY OF MOON JELLYFISH *AURELIA* SP.

IN SOUTHERN TASMANIA

IN RELATION TO ATLANTIC SALMON FARMING.

Thesis submitted by

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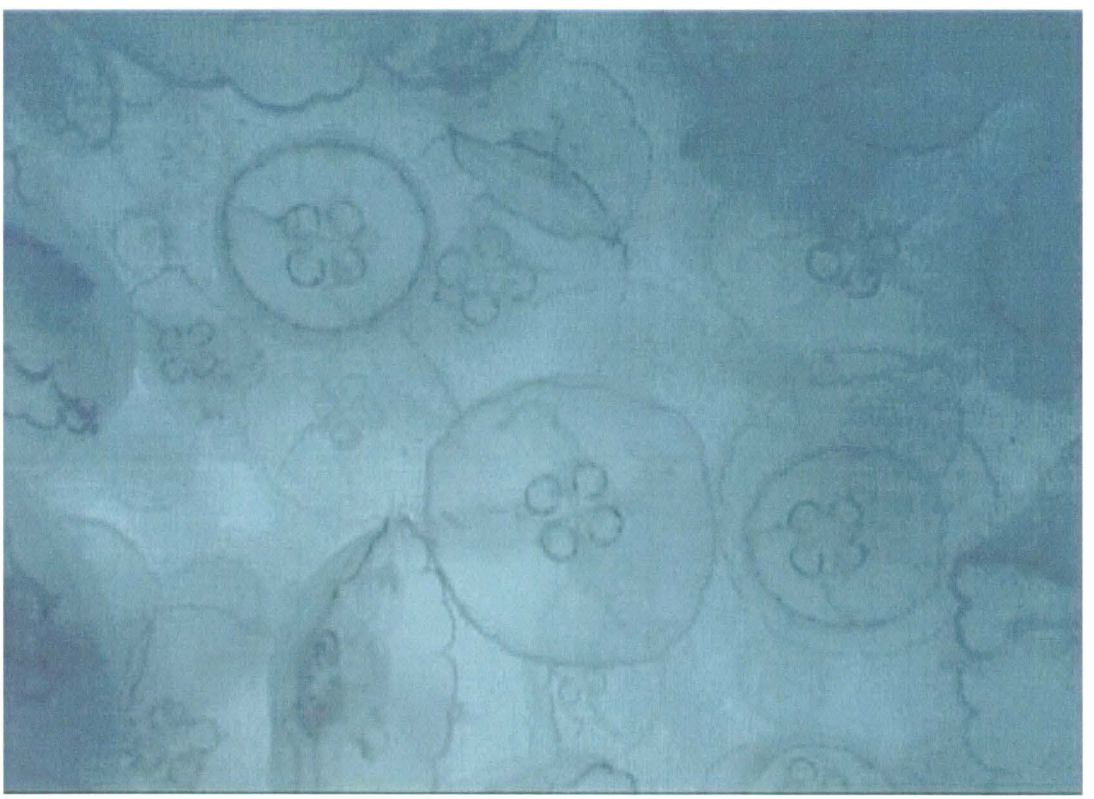

Frontispiece: *Aurelia* sp. medusae aggregation

DECLARATIONS

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Simon Trevor Willcox
January 2006

ABSTRACT

The pattern of occurrence of medusae blooms in south east Tasmania was linked to both local and global scale environmental conditions. On average, summer water temperature was over one degree warmer, local autumn rainfall was less than half, winter salinity was 0.7‰ lower, and Southern Oscillation Index (SOI) values in winter, spring, and summer were 10 – 12 points higher (and positive) in years where blooms occurred compared to those where they did not. The amount of local rainfall in autumn and the mean SOI value in winter were identified as the most useful environmental variables for predicting which summers will have medusae blooms.

Blooming *Aurelia* sp. medusae were studied in the Huon Estuary from early December 2002 to late January 2003. Medusae grew exponentially and reached a maximum mean diameter of over 150mm in two months. Maximum mean growth rates of 7.3% body weight day^{-1} were measured before the pattern of growth broke and all medusae disappeared at the end of January. The total number of medusae in the Huon Estuary was estimated to be 169 million, with a total biomass of over 28 000 tons prior to the population senescing.

Medusae formed into dense aggregations with densities up to 270 individuals m^{-3}. Aggregations occurred in an environment with strong horizontal current sheer where surface and bottom waters often flowed in opposing directions and had velocities as high as 105 mm sec^{-1}, yet were able to maintain their integrity. Observations with underwater cameras

and by SCUBA diving revealed a complex structure with coordinated swimming of individuals within aggregations responsible for aggregation maintenance.

Scyphistomae colony dynamics were examined *in situ* in south east Tasmania. Colonies were perennial and persisted for at least three years. Strobilation was observed every year in spring, however subsequent blooms of medusae did not always develop. The density of scyphistomae in colonies was a function of both the proportion of the substrate covered by the colony and the density of individuals within discreet colony patches. These variables were negatively correlated with competition from other encrusting organisms and local rainfall, and positively correlated with water temperature.

Laboratory experiments showed that temperature and salinity affected rates of asexual reproduction. These factors resulted in numerical increases in colonies up to 150% over a 32 day period. These experiments also showed there is a trade off between increasing population size through budding at high temperatures, and increasing body size, possibly in preparation for strobilation, at low temperatures.

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TABLE OF CONTENTS

FIGURES AND TABLES

CHAPTER 1:

INTRODUCTION

1.1 BACKGROUND

Blooms of gelatinous zooplankton are an increasingly common phenomenon globally (Mills 2001, Graham *et al.* 2001, Brodeur *et al.* 2002). When blooms occur they can have significant ecological, economic and societal impacts (e.g. Kakinuma 1975, Axiak and Civili 1987, Shiganova and Bulgakova 2000, Dawson *et al.* 2001, Sørnes and Aksnes 2004, Vargas and Madin 2004). Variations in the abundance and distribution of medusa over a range of temporal and spatial scales are thought to be due to differences in environmental conditions (Goy *et al.* 1989, Kingsford *et al.* 2000, Graham *et al.* 2001, Lynam *et al.* 2004). However, other factors thought to be important are eutrophication (Mills 1995, Arai 2001), species introduction (Mills 2001), an increasing amount of man made structure in the marine environment (Graham *et al.* 2001,Miyake *et al.* 2002), and overfishing modifying the pelagic food web (Legovic 1987, Mills 1995).

Jellyfish are important members of the pelagic community. They are voracious predators and when they occur in sufficiently large numbers they can have a major impact on the trophodynamics and community structure of the pelagic ecosystem (e.g. Roméo *et al.* 1992, Olesen 1995, Omori *et al.* 1995, Schneider and Behrends 1998, Purcell *et al.* 1999, Sørnes and Aksnes 2004, Barz and Hirche 2005). Predation on copepods and fish larvae are primary effects (Purcell *et al.* 2000, Shiganova and Bulgakova 2000, Brodeur *et al.* 2002). Equally important are secondary effects such as an increase in phytoplankton density caused by reduced grazing pressure from copepods and reduced food availability

to other components of the pelagic ecosystem (Arai 1997). Their large biomass and relatively short life span can also mean a large flux of dead medusae material to the benthos at certain times which may also impact on benthic communities (Morris *et al.* 1988, Kingsford *et al.* 2000). Despite their current prominence in aquatic ecosystems knowledge of the life cycles of jellyfish and the mechanisms leading to blooms is extremely limited (Lucas 2001).

Scyphozoans have a complex bipartite life cycle with two distinct reproductive body forms: the conspicuous pelagic medusae form with sexual reproduction, and a cryptic benthic scyphistoma (polyp) form with asexual reproduction (Figure 1.1). The reproductive strategy is unique and combines aspects of the strategies of corals, sponges, fish, insects, and flowering plants. Variation in the number of medusae present in a system can be the result of biotic or abiotic factors acting on any stage of the life cycle (review in Kingsford *et al.* 2000). Both the benthic and pelagic forms of many scyphozoan species display considerable intra-specific variability in many of their life history traits such as fecundity, size at maturity, and growth rate of the medusae (e.g. Garcia 1990, Lucas and Williams 1994, Ishii *et al.* 1995), and timing and rates of asexual reproduction of the scyphistomae (e.g. Brewer and Feingold 1991, Keen 1991, Miyake *et al.* 2002). This plasticity in the life history traits of scyphozoans is related to their indeterminate growth patterns, where growth is continuous and plastic, with individuals retaining the capacity to respond to biotic and abiotic factors throughout their lifetime. Individuals cannot simultaneously dedicate energy to growth and

reproduction without compromising survivorship, therefore plasticity of life history traits has evolved to favour individuals whose energy allocation maximises survival and fecundity (Stearns 1992).

The role of physical and biological environmental factors as origins of plasticity in the life history characteristics of *Aurelia* spp. has been the focus of many studies. Interannual variability in medusae abundance, growth rates, bell diameter, and size at maturity have been correlated with temperature and food supply (Lucas and Williams 1994, Ishii and Båmstedt 1998, Lucas and Lawes 1998). *Aurelia* medusae growth rates can be rapid when conditions are favourable (Möller 1980a, b, Lucas and Williams 1994), however a plastic reproductive strategy enables maturation and sexual reproduction to occur at a smaller size when growing conditions are less favourable (e.g. Schneider and Behrends 1994, Lucas 1996, Lucas *et al.* 1997, Båmstedt *et al.* 2001).

The benthic phase of the life cycle is of particular importance. It is perennial and enables populations to survive through years when recruitment to the sexual phase fails, and provides the opportunity to greatly increase the population size (Keen 1991). The abundance and distribution of the scyphistomae at the time of strobilation can directly contribute to the abundance and distribution of the bloom forming medusae (Brewer and Feingold 1991, Lucas 2001, Mills 2001, Watanabe and Ishii 2001, Colin and Kremer 2002). Therefore, an understanding of the population dynamics of the benthic stage and how the life history characteristics of this stage interact with the environment form an important component for trying to understand the observed pattern of

medusae occurrence, and the prediction of future blooms (Garrabou 1999, Colin and Kremer, 2002).

In the scyphistomae stage the allocation of energy resources to each mode of asexual reproduction can vary according to environmental conditions experienced by the scyphistomae (e.g. Keen and Gong 1989, Gong 2001). Population size and rates of bud production vary with: food availability (Coyne 1973, Gröndahl 1988a, Keen and Gong 1989), predation (Gröndahl 1988a, b,), water temperature (Coyne 1973, Kakinuma 1975), orientation of the substrate (Brewer 1978, Watanabe and Ishii 2001), density (Coyne 1973, Gröndahl 1988a), and interspecific competition (Gröndahl 1988a). The timing of strobilation and the number of ephyrae produced can be dependent on, or correlated with, changes in temperature (Rasmussen 1973), illumination (Custance 1964, Kakinuma 1975), and food availability (Spangenberg 1968, Watanabe and Ishii 2001).

In addition to occurring in large numbers in some years, *Aurelia* medusae often concentrate into dense aggregations within enclosed or semi-enclosed water bodies (e.g. Papathanassiou *et al.* 1987, Hamner *et al.* 1994, Purcell *et al.* 2000, Colombo *et al.* 2003). Although the medusa has a relatively simple physiology, it often utilises complex interactions with the biological, chemical, and physical environment (Graham *et al.* 2001). The formation of aggregations has been attributed to passive processes such as Langmuir circulation (Hamner and Schneider 1986, Larson 1992), convergences (Toyokawa *et al.* 1997, Purcell *et al.* 2000), wind, currents and tidal phenomena (Zavodnik 1987), as well as to

behavioural processes (Kingsford *et al.* 2000), including diurnal vertical migration (Toyokawa *et al.* 1997), sun-compass migration (Hamner *et al.* 1994), and active maintenance of position within a salinity gradient (Toyokawa *et al.* 1997). Aggregations are commonly thought to facilitate sexual reproduction of these gonochoristic animals (e.g. Yasuda 1971, Hamner and Jenssen 1974, Möller 1980a), although defence against predation and improved targeting of food resources have also been considered (Matanoski *et al.* 2004).

1.2 General Objectives

Despite the ecological importance of *Aurelia* spp. very little is known about the mechanisms leading to the development of large blooms of medusae. Most studies of scyphozoans to date have focused on either the benthic phase, or the pelagic phase of the life cycle, and of those that have studied both, none were *Aurelia* spp. There is a clear need to examine patterns of growth, development and reproduction in both the benthic and the pelagic phases to try and gain a clear understanding of the mechanisms leading to the observed pattern of year to year variation in abundance of the medusae. This thesis examines both phases of the life cycle and considers the observed patterns of growth and reproduction in light of key biotic and abiotic environmental factors (Figure 1.1). A population of *Aurelia* sp. found in south east Tasmania is used as a model species. The medusae stage of this species is morphologically similar to *Aurelia aurita* (Spangenberg 1965) however they are genetically distinct from other populations of *Aurelia* (Dawson et al. 2005).

The central theme of this research was to determine the mechanisms driving the intermittent development of blooms of *Aurelia* sp. medusae in south east Tasmania. This issue was addressed by researching the following key areas:

1) Investigate links between the interannual pattern of presence/absence of *Aurelia* sp. medusae blooms in south east Tasmania, and environmental conditions in those years;
2) Determine the patterns of growth, development and reproduction of the medusae stage of *Aurelia* sp.;
3) Assess the mechanisms involved in the formation and maintenance of large aggregations of *Aurelia* sp. medusae in the Huon Estuary; and
4) Describe the spatial and temporal patterns of population dynamics of the scyphistomae in the wild and the laboratory.

Initially, more detailed examination of the medusae stage was included in the research plan for this project, however, medusae were only present in one year during the project period. This prohibited between-year comparisons of population dynamics, and limited opportunity to study aggregation dynamics in the medusae stage. As a consequence, there was a shift in the emphasis of the thesis to the scyphistomae stage.

1.3 APPLIED SIGNIFICANCE

The 'moon jellyfish' has come under close scrutiny in south east Tasmania, Australia (43°S, 147°E) in recent years. A rapidly growing Atlantic salmon aquaculture industry in Tasmania has experienced

increased mortality of salmon housed in sea cages over the last decade as a consequence of large aggregations of medusae entering sea cages and releasing toxins from their nematocysts into the salmon (unpubl. data). In extreme cases the caged salmon became stressed and sank to the bottom of the sea cages where they died. Other effects included poor feeding, skin lesions, and gill necrosis that retarded growth and devalued the stock. Aquaculture companies in south east Tasmania endured mortalities of thousands of tonnes of salmon and financial losses estimated in the millions of dollars when medusae blooms occurred in three successive summers. A collaborative funding arrangement between Aquaculture industry partners and the Australian Research Council subsequently provided funding to investigate the occurrence of these large blooms of moon jellyfish in south east Tasmania.

The medusae stage occurs naturally in the coastal and sheltered waterways of this region and aggregates into dense swarms in the summer months. The species of moon jellyfish found in this region falls within the *Aurelia* clade but is genetically distinct from other *Aurelia* species (commonly *Aurelia aurita*) found in the Northern Hemisphere (Dawson *et al.* 2005).

Prior to this project very little information was available to aquaculture farm management to mitigate the financial loss to their industry through high stock mortality. There was a general concern that aggregations were preferentially forming within farm lease sites and their surrounds. Important applied aspects of the project include:

1) Developing predictive techniques for providing an 'early warning' of blooms occurring;
2) Locating and identifying the benthic stage of the life cycle and determine if farm structures are being utilised as habitat;
3) Determining if aggregations are moving purposefully within the region, and investigating if farm lease sites are targets; and
4) Making management recommendations to the salmon aquaculture industry.

1.4 Chapter Summaries

This thesis consists of a series of four discreet data chapters (Chapters 2-5), each one comprising a stand-alone manuscript, therefore there may be areas in the text that are repetitive. Each data chapter addresses the central question; "Why do blooms of medusae occur in south east Tasmania in some years and not in others?" Some referencing of other chapters in the thesis has been added to this text to assist the reader with linking the chapters together. Figure 1.1 broadly identifies the parts of the life cycle that may exhibit plasticity in response to biotic and/or abiotic environmental factors. Chapter six is a broader discussion of how the life history characteristics of *Aurelia* sp. lead to medusae blooms in south east Tasmania, and how the knowledge gained in this study contributes to our understanding of the life history strategy of the cosmopolitan *Aurelia* genus. Outlined below is a summary of the aims of each data chapter, together with a brief description of the data used to address these aims.

Chapter 2: Patterns of occurrence of *Aurelia* sp. medusae blooms, and links with the environment

Detailed records of *Aurelia* sp. medusae occurrence in south east Tasmania span the past eight years. This chapter compared the interannual pattern of presence or absence of *Aurelia* sp. medusae bloom with broad (global) and fine (local) scale environmental variables. Years with or without blooms were correlated with environmental variables. Factors with significant relationships were used to build a model to provide a prediction of the likelihood of a bloom in the following summer. The life history characteristics that were potentially affected by the environmental factors were identified and hypotheses for the mechanisms involved were developed.

Chapter 3: Population dynamics and aggregatory mechanisms of moon jellyfish, *Aurelia* sp., medusae in the Huon Estuary, Australia.

This chapter examined the pattern of growth and maturation of a large naturally occurring population of medusae within the Huon Estuary in south east Tasmania. The development of medusae in the population began when they were about 15mm diameter at the start of summer and continued until the population senesced and disappeared from the estuary toward the end of summer. Novel techniques were developed to estimate the total biomass of medusae within the estuary and to examine physical and behavioural mechanisms important in the formation and maintenance of aggregations. The evolutionary significance of this energetically expensive characteristic of the medusae population is discussed.

Chapter 4: Population dynamics of *Aurelia* sp. scyphistomae in south east Tasmania, Australia

The aim of this chapter was to examine the spatial and temporal patterns in the population dynamics of the scyphistomae stage of the life cycle *in situ*, and to identify potential environmental influences over the two modes of asexual reproduction and mortality. Naturally occurring colonies were monitored for two years. Growth dynamics were compared with season and local-scale environmental factors. The additional use of artificial substrates *in situ* enabled density dependent effects to be reduced in colonies and the development of a better understanding of environmental factors on asexual reproduction, habitat utilisation, and interspecific competition.

Chapter 5: Effects of temperature and salinity on asexual reproduction of scyphistomae of *Aurelia* sp.: an experimental study.

Temperature and salinity were implicated as key environmental factors playing a role in determining the annual presence or absence of medusae based on the dynamics of naturally occurring colonies (Chapter 4) and records of medusae bloom occurrence (Chapter 2). This chapter experimentally quantified the effect of temperature and salinity on asexual reproduction in the scyphistomae. This approach provided information about the relative importance of budding and somatic growth in the scyphistomae, and allowed development of a more complete picture of the reproductive strategy of *Aurelia* sp.

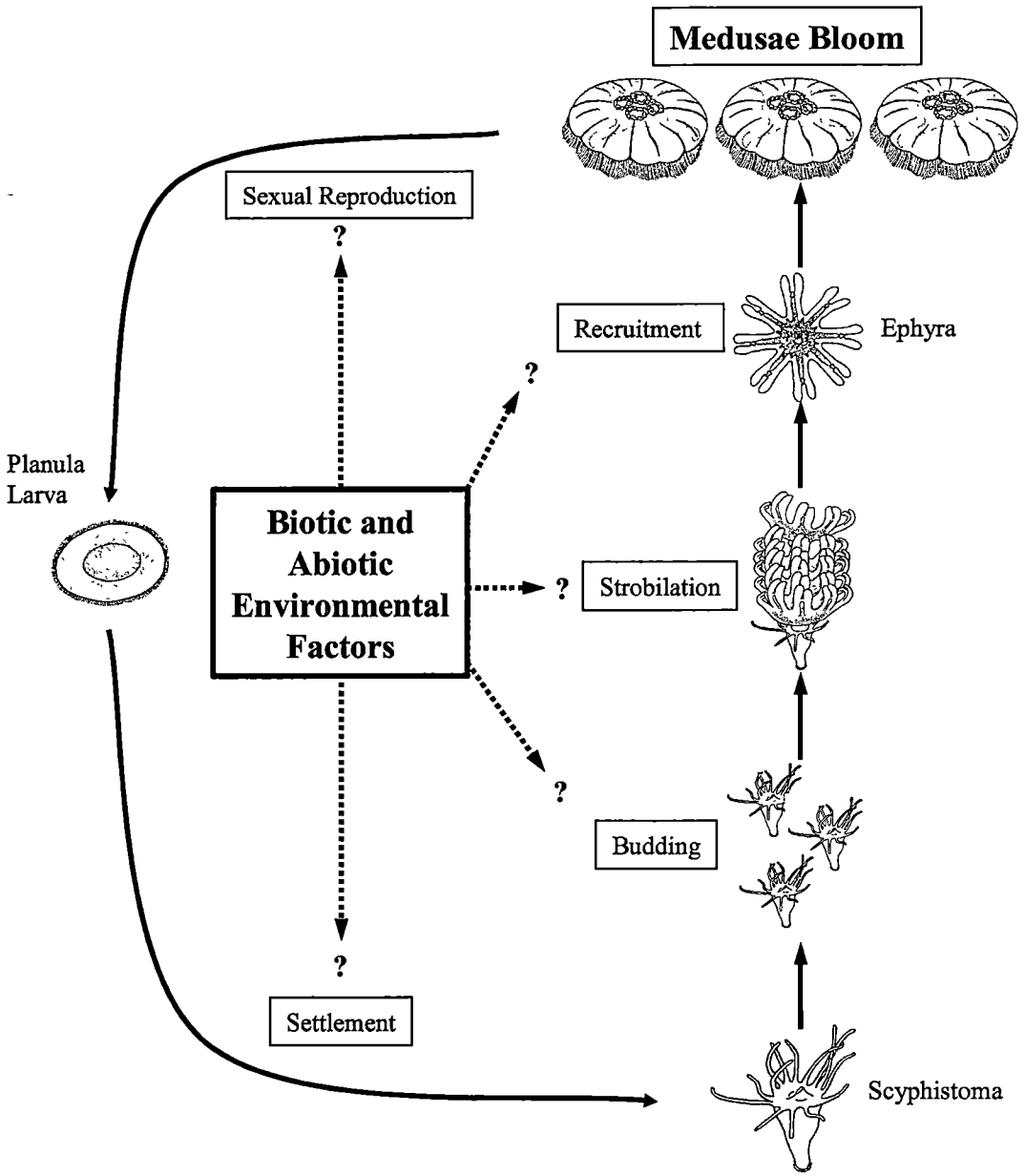

Figure 1.1 Summary of the common life cycle of *Aurelia* spp. indicating the life history stages where biotic and abiotic environmental factors may be acting to contribute to the observed spatial and temporal patterns of blooms of *Aurelia* sp. medusae in south east Tasmania.

CHAPTER 2:

PATTERNS OF OCCURRENCE OF *AURELIA* SP. MEDUSAE BLOOMS, AND LINKS WITH THE ENVIRONMENT

2.1 INTRODUCTION

Jellyfish abundance is increasing in marine ecosystems worldwide (Mills 2001, Lynam *et al.* 2004). When medusae are abundant they can modify the species composition and abundance of the zooplankton community through grazing pressure (e.g. Behrends and Schneider 1995, Finenko *et al.* 2003, Purcell 2003, Barz and Hirche 2005). This impact can extend to all trophic levels through 'top down' and 'bottom up' control mechanisms (e.g. Shiganova and Bulgakova 2000, Brodeur *et al.* 2002, Kideys 2002). In addition, jellyfish can play an important role in the flow of energy through the pelagic food web (Shushkina and Musayeva 1983) and form an important component in the flux of organic matter to bottom sediments (Morris *et al.* 1988, Kingsford *et al.* 2000). A further consequence of large blooms of *Aurelia* sp. medusae in south east Tasmania is an elevated mortality among Atlantic salmon held in sea-cage aquaculture facilities within the region with a significant associated financial burden.

Extreme interannual variability in the occurrence of blooms of gelatinous zooplankton populations is a common phenomenon (e.g. Hernroth and Gröndahl 1985a, b, Schneider and Behrands 1994, Young *et al.* 1996, Purcell *et al.* 1999b, Lucas 2001). Medusae population size in any year is determined by the abundance of scyphistomae, the number of ephyrae produced, and the survival of ephyrae (Purcell *et al.* 1999b), and these are linked to environmental conditions. Environmental conditions correlated with jellyfish abundance include local scale factors such as temperature (Brewer and Feingold 1991, Lynam *et al.* 2004), salinity

(Purcell *et al.* 1999b), wind strength (Harris *et al.* 1991, Lynam 2004), stratification (Raskoff 2001) and circulation (Barz and Hirche 2005); and globalscale factors such as: the southern oscillation index (SOI) (Young *et al.* 1993, Harris *et al.* 1991) and the north Atlantic oscillation index (NAOI) (Goy *et al.* 1989, Lynam *et al.* 2004).

Blooms of *Aurelia* sp. medusae occur in the sheltered waterways of south east Tasmania in some years but not in others. Primary production, the composition of the plankton community (e.g. Clementson *et al.* 1989, Harris *et al.* 1988, 1991) and the recruitment success of fish (e.g. Harris *et al.* 1988, Thresher *et al.* 1989) and cephalopods (Pecl *et al.* 2004) have been linked to environmental conditions in these waters. With such potential for blooms of jellyfish to modify the trophic structure of ecosystems and the additional economic costs to some industries, it is important to understand the role that climate forcing plays in determining the presence of large numbers of medusae in any year. However, despite their ecological importance, the current understanding of the mechanisms governing the temporal pattern of occurrence of jellyfish blooms remains poor.

This project aims to determine if predictive relationships can be established between the pattern of occurrence of *Aurelia* sp. medusae blooms in summer and local and global-scale environmental conditions recorded in the preceding seasons (autumn, winter and spring). It also aims to develop hypotheses about which part or parts of the life cycle may be critically affected by environmental conditions, and possible mechanisms involved. Ultimately, environmental conditions that are

associated with medusae bloom occurrence will be used to develop a predictive model that provides an estimate of the probability of a medusae bloom developing in the following summer. This will be particularly valuable for managers of Atlantic salmon sea-cage aquaculture facilities looking to reduce mortality of their stock. These data are also discussed in the context of the decadal time scale climatic and environmental cycle of the ENSO (El Niño, Southern Oscillation) phenomenon (van Loon and Shea 1985).

2.2 METHODS

Atlantic salmon aquaculture industry records from operations based in the sheltered waters of the Huon Estuary and the D'Entrecasteaux Channel provided data on the occurrence of blooms of medusae in summers during an eight year period from 1997/98 to 2004/05 (Fig 1). Robust quantitative data about the abundance and distribution of *Aurelia* sp. medusae in south east Tasmania are scarce. Industry only reliably records the presence of *Aurelia* sp. medusae when they occur at densities high enough to cause a problem with caged fish health. Using these data, it was only possible to identify a year as having jellyfish in bloom proportions (medusae 'present') or not having jellyfish in bloom proportions (medusae 'absent'). Medusae may have been present in low densities in years where blooms were recorded as absent, and quantitative information about the abundance in each year was unavailable. No reliable records of *Aurelia* sp. occurrence were available prior to the summer of 1997/98.

Environmental records were used to determine the association of these parameters with bloom presence or absence. Environmental factors used were restricted to routinely collected and readily available data sets to facilitate simple and economic use of the predictive model and were: mean seasonal wind direction; mean seasonal wind speed; total seasonal rainfall; mean seasonal southern oscillation index (SOI) values; mean seasonal water salinity; monthly mean water temperature; monthly mean air temperature and weekly values from a 30 day moving average of the water temperature. Seasons were defined as: Summer, December-February; Autumn, March-May; Winter, June-August; and Spring, September-November. All references to 'years' in this chapter refer to 'biological years'. These are nominally defined as the 12-month period starting on the 1st of March in each year to align with the recognised timing of the seasons. Blooms of *Aurelia* sp. medusae occurred in south east Tasmania during summer and had disappeared from the system by the end of the biological year.

Wind strength, wind direction, and air temperature data recorded at three-hourly intervals at Cape Bruny light house, and 24 hour total rainfall to 0900 recorded at Margate weather station were obtained from Australian Bureau of Meteorology weather station records (Figure 2.1). While these records are not a perfect measure of conditions throughout south east Tasmania, they do reflect the broad features of seasonal and interannual variability in the region. Daily mean water temperature and salinity data were obtained from the environmental monitoring records routinely collected by the TASSAL Atlantic salmon aquaculture company

in south east Tasmania (Figure 2.1). These data were daily averages generated from twice daily measurements at three meters water depth measured to one decimal place using hand-held YSI digital temperature/salinity meters recorded at four separate lease sites situated in the Huon Estuary.

The SOI is a simple description of the air pressure shift between the Asian and South Pacific regions. This shift is described in terms of the strength and direction of the shift. Southern Oscillation Index values close to zero indicate neutral conditions close to the long term average. Southern Oscillation Index values were calculated as follows:

$$SOI = 10\frac{[Pdiff - Pdiffav]}{SD(Pdiff)}$$

where Pdiff = (average Tahiti mean sea level pressure for the month)-(average Darwin mean sea level pressure for the month), Pdiffav = long term average of Pdiff for the month in question, and SD(Pdiff) = long term standard deviation of Pdiff for the month in question.

The biology of south east Tasmania coastal waters has been linked with both the number and the strength of westerly wind events across the region (Harris *et al.* 1988, 1991). The studies by Harris *et al.* (1998, 1991) they generated a westerly wind ratio using synoptic pressure charts, however the method used in this study differed in that actual wind readings were used to generate the ratio. The westerly wind ratio was calculated by dividing the number of readings with a westerly component (bearing between 225°T and 315°T) by the number of readings with a non-

westerly component (bearing >315°T or <225°T). Tallying the number of recordings where wind velocities were ≥force eight on the Beaufort scale generated a relative measure of the 'windiness' of any season.

Two-way ANOVA was used to compare monthly and seasonal means. Monthly total rainfall data were log10 transformed to remove heterogeneity of variance. Within-season planned contrasts were used to identify seasons with difference when significant differences were found. One-way ANOVA was used to compare summer maximum temperatures and to compare winter minimum temperatures. A repeated measures ANOVA was used to compare the rate of change of water temperature among years with and without medusae during the period where ephyrae are developing into juvenile medusae in the plankton. This occurs each year in spring in south east Tasmania each year (unpubl. data). These data were smoothed with a 30 day moving average prior to analysis.

Discriminant function analysis was used on environmental data to determine which variables, and which seasons, differentiated between years where medusae were present and absent. Environmental data used were seasonal means of variables identified by ANOVA as being different among years where medusae were present and absent. Only data from the period prior to the time medusae are normally seen in each biological year was used in this analysis as the purpose was to develop a predictive function for future blooms of *Aurelia* sp. The prior probability of any year having medusae present or absent was set at 0.5 based on the relative frequency of observations (years) with and without medusae. The model was cross validated by comparing the predicted and the observed

occurrence of medusae blooms for each of the years of data used to generate the model.

For prediction, the discriminant function coefficients generated by this analysis are used in the linear discriminant equation:

$$D=B_0+B_1X_1+B_2X_2+...+B_pX_p$$

where X is the value of each independent variable and B is the coefficient estimated from the data for each independent variable.

Normal probability theory can be used to determine the probability of the 'D' score belonging to the 'medusae present' distribution or the 'medusae absent' distribution.

2.3 RESULTS

Aurelia sp. medusae were recorded by the salmon industry as being present in the Huon Estuary and D'Entrecasteaux Channel in four of the eight years from 1997/98 to 2004/05; 1998/99- 2000/01 and 2002/03.

Maximum monthly mean temperatures were 16-17.5°C. Water temperatures were around one degree warmer in summers with medusae blooms (17.4°C ±0.1 (se)) than in years where blooms were absent (16.3°C ±0.1 (se)). Minimum monthly mean temperatures were 10.8-11.9°C. There were no differences in minimum temperatures between years with and without medusae blooms (Figure 2.2, Table 2.1). The pattern of air temperature was similar to that for water temperature with summer maximum temperatures around one and a half degrees warmer (16.5°C ±0.12 (se)) in years where medusae blooms were present

than in years where medusae blooms were absent (15°C ±0.12 (se)). Again, winter minimum temperatures were not different between years with and without medusae blooms (Figure 2.2, Table 2.1). The rate of increase of water temperatures through spring was not different between years with and without medusae blooms ($F = 0.2$, $df = 9,54$, $P = 0.9$) (Figure 2.3). This was primarily due to the lack of a relationship between winter minimum temperature and the occurrence of blooms.

The occurrence of medusae blooms was not related to the proportion of time the wind was from the west quadrant in any season (Figure 2.4, Table 2.2). Similarly, the mean strength of wind recordings was not related to bloom presence or absence in any season (Figure 2.5, Table 2.2).

The SOI was higher and positive in the winter and spring prior to medusae blooms, and in the summer period following bloom development than in years where blooms were absent. There was no difference in the SOI in autumn between years with and without medusae blooms (Figure 2.6, Tables 2.2 & 2.3).

The total amount of autumn rainfall in years with medusae blooms was around half that of years without blooms. There was no difference in total seasonal rainfall between years with and without medusae blooms in winter, spring, or summer of those years (Figure 2.7, Tables 2.2 & 2.3).

Mean salinity in winter was around 0.6‰ lower in years with medusae blooms than in years without, but there were no differences in the autumn, spring or summer of those years (Figure 2.8, Tables 2.2 & 2.3).

Total autumn rainfall, mean winter salinity, mean winter SOI values, and mean spring SOI values were the variables that were different among years preceding summers when *Aurelia* sp. medusae were present and years when medusae were absent. Variables found to be different among years in summer (maximum air and water temperature, summer SOI) were not used as they occur after the time when medusae first appear and were not useful for the purpose of prediction. Discriminant function analysis using these variables showed that environmental conditions in years when medusae were present were different to the conditions in years where medusae were absent (Wilks' Lambda, $\chi^2 = 10.838$, df = 2, P = 0.004). This analysis showed the variables contributing to the greatest divergence in the discriminant function score were total rainfall in autumn and SOI values in winter (Table 2.4). Winter salinity and spring SOI values did not explain any additional variation and were excluded during the analysis. Discriminant function scores >0 (mean = 2.16, SD = 0.9) were associated with years when medusae were absent, while scores <0 (mean = -2.16, SD = 1.09) were associated with years when medusae were present (Figure 2.9). Cross validation of the predictive function using actual independent variable values resulted in 100% of cases being correctly classified.

2.4 Discussion

The occurrence of blooms of *Aurelia* sp. medusae in south east Tasmania's estuarine environment was variable among the years

examined. This is a common feature among scyphozoan populations globally (e.g. Hernroth and Gröndahl 1985a, b, Schneider and Behrands 1994, Purcell *et al.* 1999b). The presence or absence of medusae blooms was linked to both local and global scale climatic and environmental variables. Blooms occurred in summer of years with higher temperatures in summer, lower rainfall in autumn, lower salinity in winter and positive SOI values through winter, spring and summer. These data are not sufficient to determine the exact mechanisms for environmental control of medusae abundance in south east Tasmania, however, several possible explanations which may account for observed interannual differences are proposed.

The presence of medusae blooms in any summer is the result of the functioning of several key aspects of the life cycle. In *Aurelia* these include: the rate of budding of the benthic scyphistomae during autumn, winter and spring; the rate of strobilation at the start of spring to produce the free-swimming juvenile medusae (ephyrae); and the survival rate of ephyrae through spring to recruit to the medusae population (Spangenberg 1967, 1968, Lucas 2001). Modified rates of any of these processes could lead to the observed presence or absence of medusae blooms in south east Tasmania (Båmstedt *et al.* 2001, Lucas 2001). Environmental conditions can influence the life cycle either directly or indirectly at a single critical stage, or at several stages. For example, high rainfall in autumn and high salinity in winter could have acted directly, or indirectly, on the scyphistomae stage to result in fewer ephyrae being produced, but autumn and winter conditions could only

have acted indirectly on the ephyrae stage because strobilation occurs in spring in south east Tasmania, after those conditions had occurred.

This study found salinity in winter to be negatively correlated with the occurrence of blooms of *Aurelia* sp. medusae. Factors affecting scyphistomae population size can have a major impact on the size of the medusae population in the following season (e.g. Hernroth and Gröndahl 1985a, b, Gröndahl 1988a, Colin and Kremer 2002, Osman and Whitlatch 2004). Expansion in the range of *Aurelia aurita* medusae in a Finnish Fjord (Palmen 1953) and the Sea of Azov (Zakhutsky *et al.* 1983) have also been related to changes in salinity, however, "remarkable tolerance to salinity" in the scyphistomae of *A. aurita* has also been reported (Halisch 1935). This suggests that salinity may have been acting indirectly rather than directly on the scyphistomae during the period prior to strobilation.

This project did not find a relationship between medusae bloom occurrence and temperatures prior to strobilation in spring, however the relationship with salinity in the period immediately prior to strobilation indicates reduced strobilation due to high salinity may have been a potential mechanism mediating bloom occurrence in south east Tasmania in some summers. The total number of ephyrae produced is also dependent on the number of ephyrae produced per individual scyphistomae. In scyphozoans, reduced ephyrae production per scyphistomae occurs in direct response to parameters such as temperature (Brewer and Feingold 1991, Lucas and Williams 1994, Purcell *et al.* 1999b), salinity (Purcell *et al.* 1999b), and food availability

(Chen *et al.* 1985, Hernroth and Gröndahl 1983, 1985a, Gröndahl 1988a, b, Keen 1991). Clearly, the effect of salinity on the population dynamics of the scyphistomae of *Aurelia* sp. is one that requires clarification through further study. Chapter Four in this thesis examines the population dynamics of the scyphistomae stage *in situ* over a two year period, while Chapter Five details aquarium experiments examining the responses of the scyphistomae to the salinity and temperature regimes likely to be experienced by scyphistomae *in situ* in south east Tasmania.

The recruitment period from newly released ephyrae to juvenile medusae takes several months in *Aurelia* sp. and occurs in spring. In this study no links were found between bloom occurrence and the local scale environmental factors experienced by the ephyrae. Very little is known about processes driving ephyrae survival and development, and although mortality of ephyrae and medusae prior to maturation is thought to be low (Schneider 1989), prey abundance and prey variety during development may be important for survival (Sullivan *et al.* 1997, Båmstedt *et al.* 2001). In south east Tasmania there may be up to three months difference in the timing of the onset of the spring bloom, and up to three orders of magnitude difference in plankton biomass (Harris *et al.* 1988, 1991). Any delay in the spring bloom or an absence of suitable prey types in the plankton around this time may have an adverse effect on ephyrae growth and development (Goy *et al.* 1989, Båmstedt *et al.* 2001, Lynam *et al.* 2004).

There is increasing awareness of the role that broad scale spatial and temporal patterns such as the Southern Oscillation Index (SOI) and

the north Atlantic Oscillation Index (NAOI) play in influencing local-scale environmental and biological conditions through large scale oceanic-atmospheric coupling processes (e.g. Chavez *et al.* 1999, Gonzalez *et al.* 2000, Marshall *et al.* 2001, Ottersen *et al.* 2001, Perry *et al.* 2004). Westerly wind stress and westerly wind drift in the southern ocean are linked to the latitudinal position of the high-pressure band over mainland Australia and hence the SOI (van Loon 1972a, b, van Loon and Shea 1985).

In south east Tasmania large-scale oceanographic circulation and westerly wind frequencies are important in controlling the timing and productivity of the spring phytoplankton bloom in shelf waters (Harris *et al.* 1991) through repeated deep mixing of shelf waters (Clemmentson *et al.* 1989, Harris *et al.* 1987, 1988). This has in turn been linked with the species composition and abundance of the zooplankton, and to the recruitment success of marine fish (e.g. Thresher *et al.* 1989, Young *et al.* 1993, Thresher 1994, Perry *et al.* 2004), molluscs (Young *et al.* 1992) and crustaceans (Pearce and Phillips 1988, Harris *et al.* 1988). In the North Sea, the NAOI has also been linked to patterns of wind stress and the subsequent timing and abundance and species composition of the spring phytoplankton and zooplankton blooms (Edwards *et al.* 2002, Reid *et al.* 2003). It is possible that a deep (50m) channel extending from the southern end of the Huon Estuary and D'Entrecasteaux Channel out toward the continental shelf acts as a conduit for shelf waters to enter these areas (CSIRO 2000). In this way conditions on the shelf, which are responding to the broad-scale oceanographic-atmospheric patterns (i.e. as

represented by the SOI), may be communicated to the environment of the scyphistomae and developing ephyrae.

Physical conditions in the water column can also account for high mortality of the fragile ephyrae or transport of ephyrae out of the system (Raskoff 2001, Lynam *et al.* 2004, Barz and Hirche 2005). Westerly weather can bring gale force winds and heavy rain to southern Tasmania (Harris *et al.* 1988). These conditions can result in strong wind driven surface currents, water column overturning and sudden reductions in salinity in the surface layer (e.g. CSIRO 2000, Cheshuck 2001), however the short duration of these events means they may not have been detected by the method of analysis used in this study. Close monitoring of ephyrae populations *in situ* in association with these types of conditions would be required to determine the susceptibility of the ephyrae stage to these types of mechanisms.

The occurrence of medusae blooms in south east Tasmania is linked to a large scale atmospheric phenomenon which has a 11-12 year cycle (van Loon and Shea 1985, Harris *et al.* 1988, Marshal *et al.* 2001, Tang *et al.* 2003). Young *et al.* (1996) noted the abundance of gelatinous zooplankton in south east Tasmania shelf waters to be linked to the 11-12 year El Niño and southern oscillation (ENSO) phenomenon, while scyphomedusae outbreaks elsewhere have also been linked to similar large scale atmospheric phenomena sharing similar long term cycles (e.g. Goy *et al.* 1989, Brodeur *et al.* 1999, Dawson *et al.* 2001, Ottersen 2001, Lynam *et al.* 2004). If the high SOI values associated with more frequent blooms of *Aurelia* sp in the 1998/99 to 2001/02 period represent the 'peak'

of this 11–12 year cycle then similarly frequent medusae bloom occurrence to those experienced recently in south east Tasmania might be expected again through a five year period starting around 2008 with a continuing low frequency of bloom years in the meantime. Clearly longer term monitoring of the occurrence of blooms of *Aurelia* sp. medusae is required to confirm any relationship with these longer term patterns.

This study has shown that links exist between local and global-scale environmental conditions and the interannual pattern of occurrence of blooms of the ecologically important scyphozoan, *Aurelia* sp. Total rainfall in autumn and SOI values through winter were shown to be the best predictors of blooms of *Aurelia* sp. medusae in south east Tasmania. These predictors are remarkably similar to those found for the scyphozoan medusae *Pelagia noctiluca* in the western Mediterranean Sea where rainfall and atmospheric pressure are amongst the best predictors for bloom occurrence (Goy *et al.* 1989). Elsewhere, temperature, salinity, atmospheric pressure and the North Atlantic Oscillation Index (NOAI) have also been linked to interannual variability of scyphozoan medusae (Graham 1994, Graham *et al.* 2001, Lynam *et al.* 2004). These results provide further evidence of the role played by large-scale climatic conditions in influencing physical and biological conditions at the local scale, and suggests that the occurrence of medusae blooms in south east Tasmania is in fact part of a larger pattern of global synchrony (Perry *et al.* 2004).

It is clear that mechanisms operating on the life cycle of *Aurelia* sp. are complex and that environmental conditions may be acting indirectly

through other unmeasured variables. This study has helped develop a clearer understanding of the dynamic relationships that are operating in marine and estuarine ecosystems, and has facilitated the formation of hypotheses essential to directing further study of the patterns of medusae bloom occurrence and the relative importance of each life history stage. Furthermore, the predictive model developed in this study provides the Atlantic salmon sea-cage aquaculture companies in south east Tasmania with a valuable tool that may be used in management decisions aimed at reducing mortality of caged fish stocks and reduction of financial costs to the industry in years where medusae blooms are forecast.

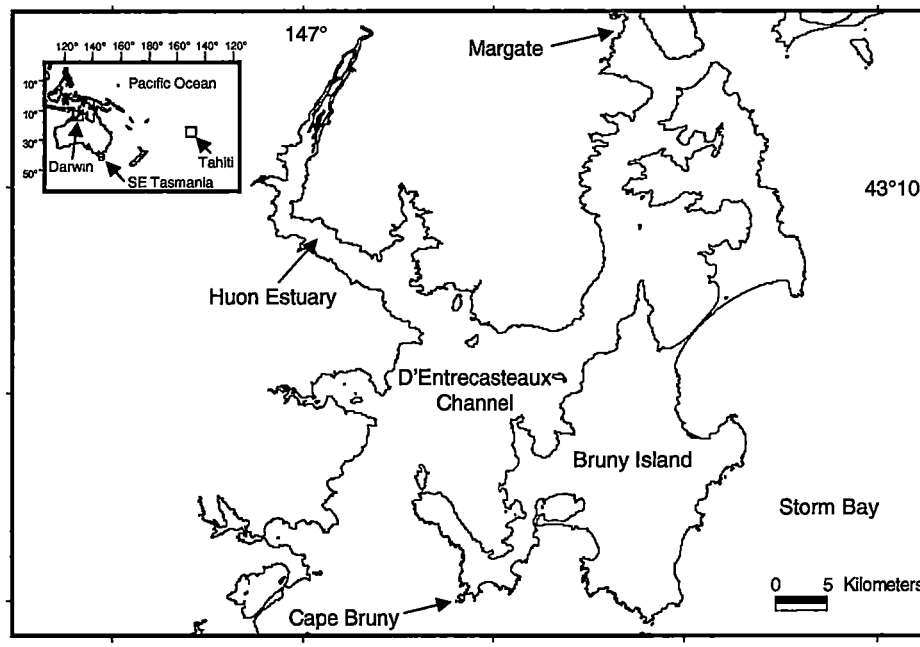

Figure 2.1 Location of the Huon Estuary and the D'Entrecasteaux Channel in south east Tasmania, Australia.

Table 2.1 Results of ANOVA of environmental factors grouped by season and by presence or absence of medusae in that year. * represents significant differences between years with medusae blooms and years without medusae blooms. df 1,7 for all ANOVAs.

Factor	Season	F	P
Maximum Water Temperature	Summer	100	<0.001*
Minimum Water Temperature	Winter	0.6	0.5
Maximum Air Temperature	Summer	37.5	0.001*
Minimum Air Temperature	Winter	1.1	0.3

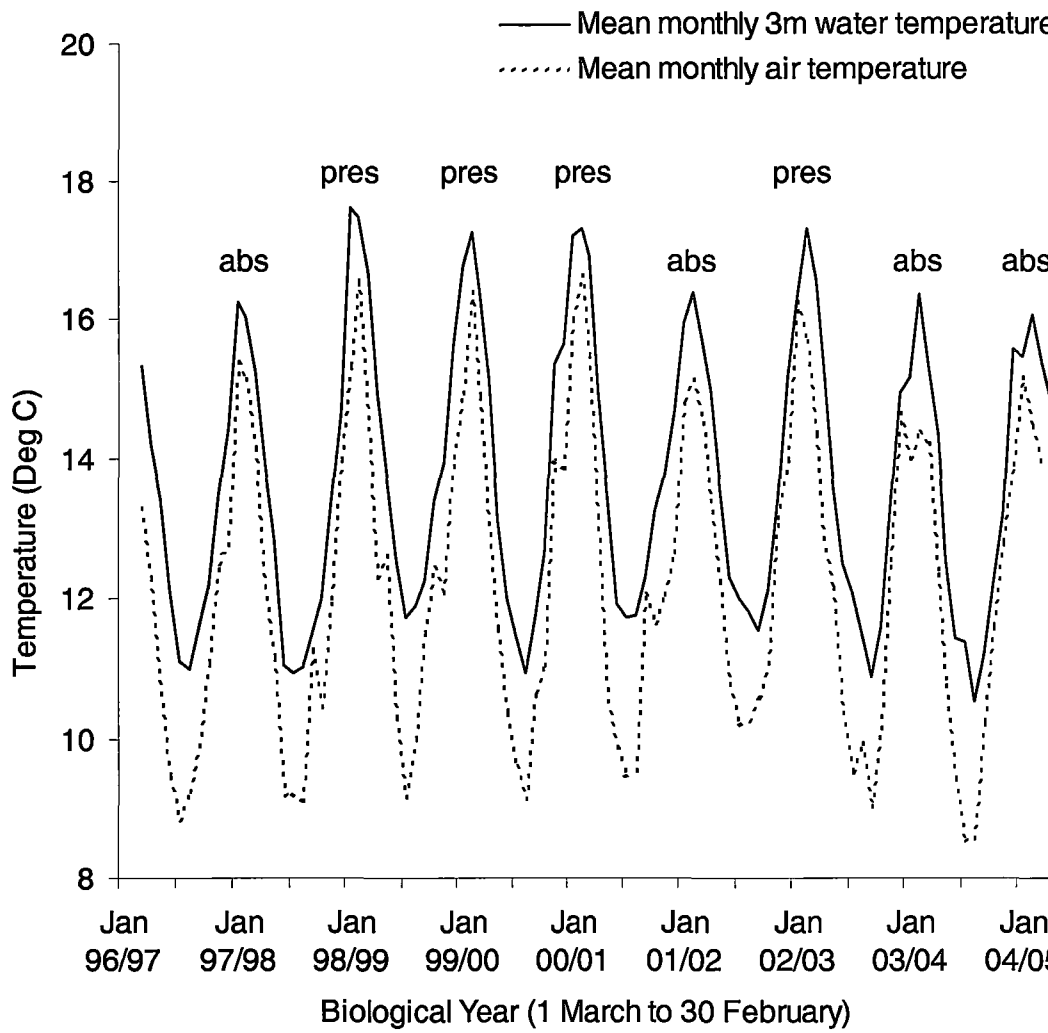

Figure 2.2 Mean monthly temperature time series. The solid line depicts mean water temperature at three metres in the Huon Estuary (Figure 2.1). The dashed line depicts mean air temperature at Cape Bruny weather station (Figure 2.1). "pres" indicates summers where *Aurelia* sp. medusae were present in the Huon Estuary and "abs" indicates summers where medusae were absent from the Huon Estuary.

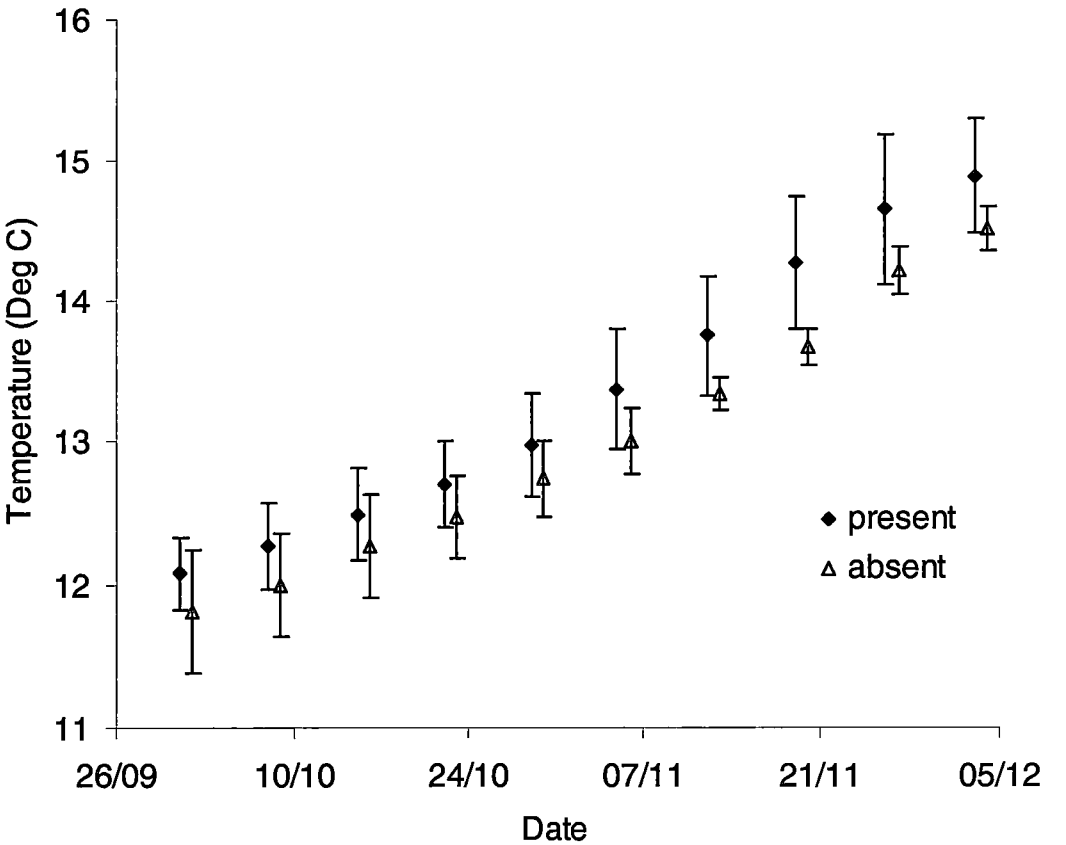

Figure 2.3 Mean water temperatures (±se) at 3m in the Huon Estuary during the spring period of rapid warming. Data are weekly values of a 30 day running average. Open triangles depict temperatures in years where *Aurelia* sp. medusae were absent and closed diamonds depict temperatures in years where medusae were present. 'Present' data are offset by one day to enable both sets of data to be viewed.

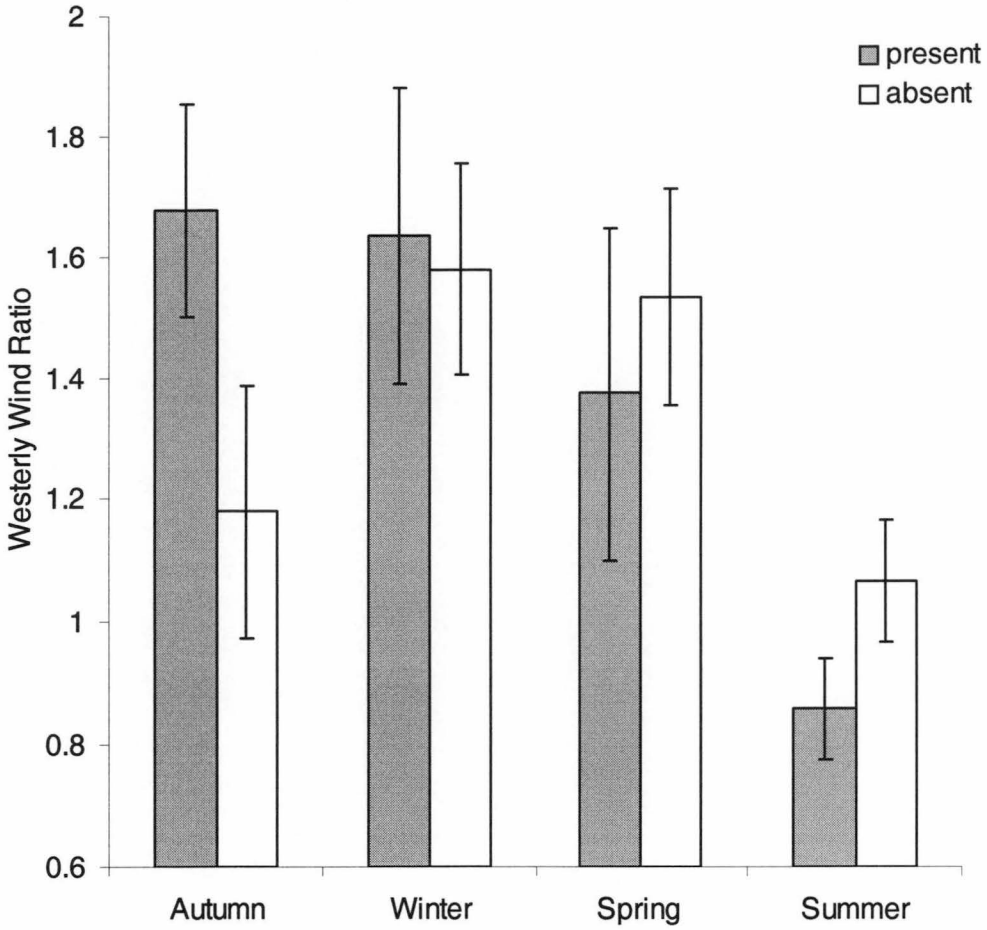

Figure 2.4 The mean ratio of the number of observations where wind was from the west (180-360° T) to the number of observations where the wind was from the east (0-180° T) (±se) for each season in years where *Aurelia* sp. medusae were present (shaded) and where medusae were absent (white). Medusae and non-medusae years were not significantly different in any season.

Table 2.2 Results of two-way ANOVAs of environmental factors grouped by season and by presence or absence of medusae in that year. * represents significant differences between years with medusae blooms and years without medusae blooms.

Factor	F	df	P
Westerly wind ratio	0.1	1,24	0.7
Number of days where wind was ≥ force eight	0.9	1,24	0.4
Southern Oscillation Index	21.2	1,88	<0.001*
Rainfall (log10 transformed data)	6.2	1,84	0.015*
Salinity	5.6	1,385	0.016*

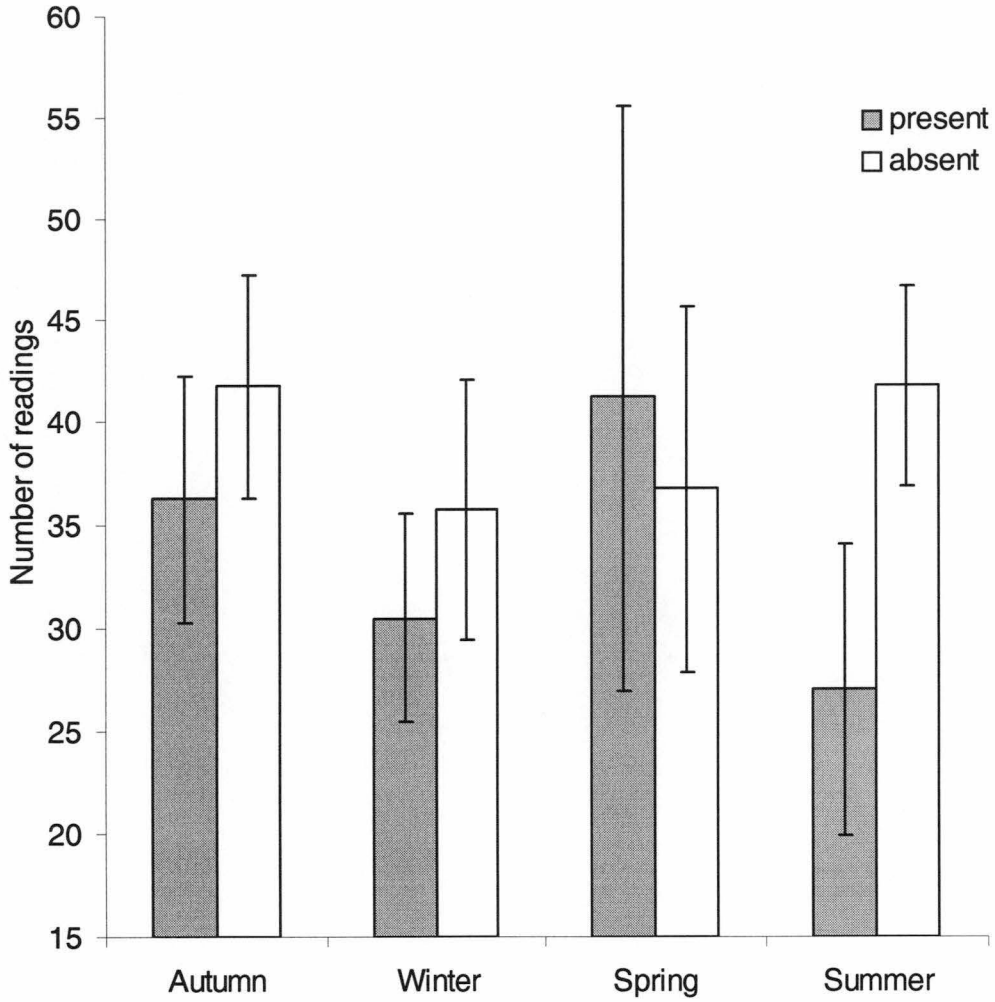

Figure 2.5 Mean number of observations (±se) where wind speed was greater force eight and above on the Beaufort scale for each season in years where *Aurelia* sp. medusae were present (shaded) and where medusae were absent (white). Medusae and non-medusae years were not different in any season.

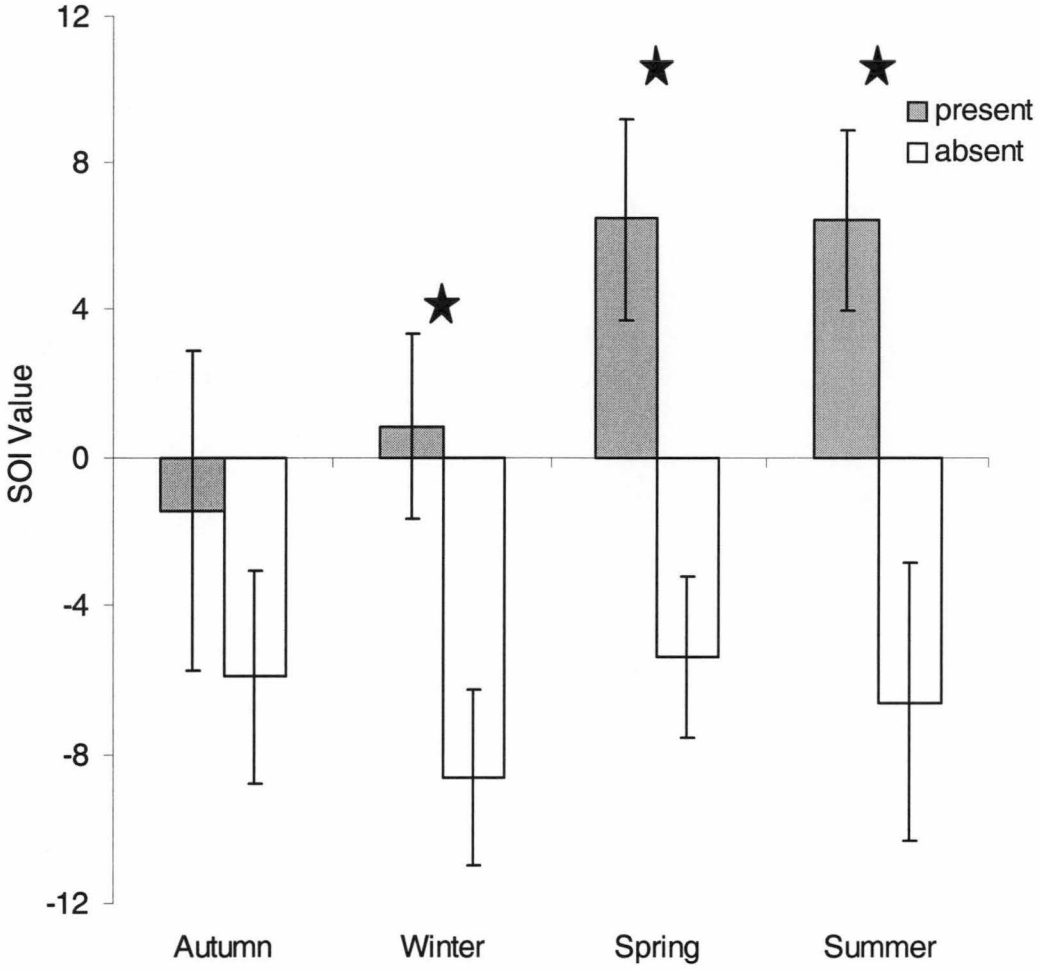

Figure 2.6 Mean Southern Oscillation Index (SOI) values (±se) for each season in years where *Aurelia* sp. medusae were present (shaded) and where medusae were absent (white). * represents where medusae and non-medusae years were different ($P < 0.05$).

Table 2.3 Results of within-season planned contrasts of environmental factors between years with and without medusae blooms. * represents significant differences between years with medusae blooms and years without medusae blooms.

Factor	Season	F	df	P
Southern Oscillation Index	Autumn	0.7	1,22	0.4
	Winter	7.6	1,22	0.01*
	Spring	11.5	1,22	0.003*
	Summer	8.4	1,22	0.008*
Rainfall (log10 transformed data)	Autumn	8.2	1,22	0.009*
	Winter	1.4	1,22	0.3
	Spring	0.1	1,22	0.8
	Summer	2.1	1,22	0.2
Salinity	Autumn	1.3	1,93	0.3
	Winter	10.7	1,93	0.001*
	Spring	2.2	1,93	0.1
	Summer	2.4	1,93	0.1

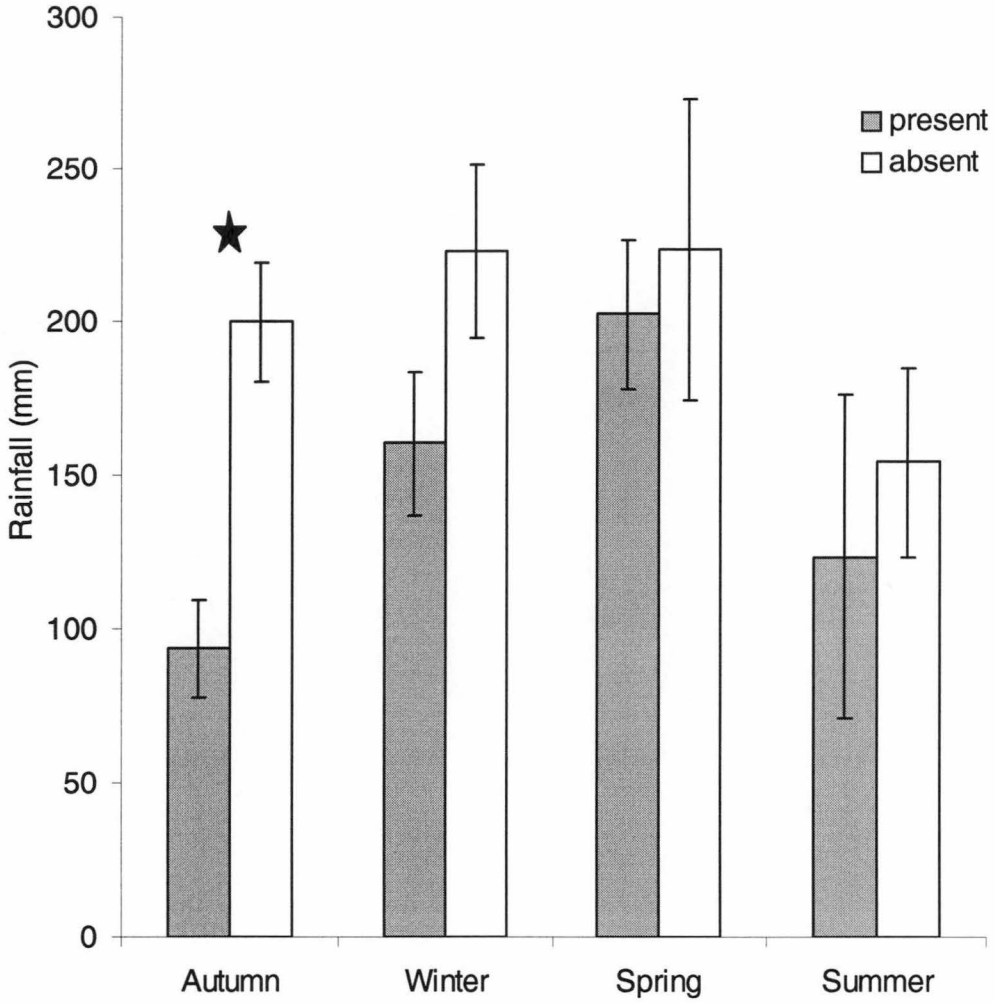

Figure 2.7 Mean total rainfall for each season (±se) in years where *Aurelia* sp. medusae were present (shaded) and where medusae were absent (white). * represents where medusae and non-medusae years were different ($P < 0.05$).

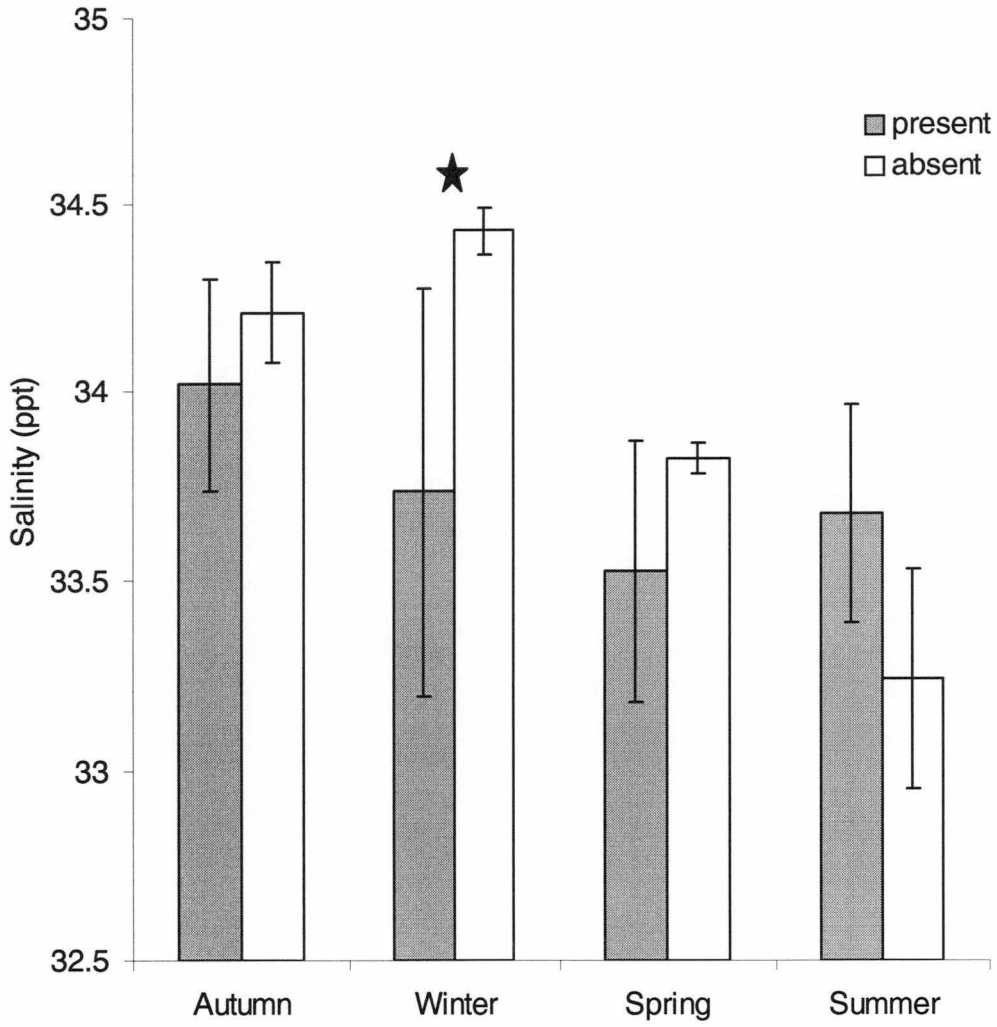

Figure 2.8 Mean salinity (±se) at 3m below the surface for each season in years where *Aurelia* sp. medusae were present (shaded) and where medusae were absent (white). * represents where medusae and non-medusae years were different ($P < 0.05$).

Table 2.4 Discriminant function coefficients for the environmental characters found to be different between years with or without medusae, and the Constant Coefficient for use in the predictive function equation (methods).

Environmental Parameter	Discriminant Function Coefficient
Total Autumn Rainfall	3.13
Mean Winter SOI value	-0.13
Constant	-5.568

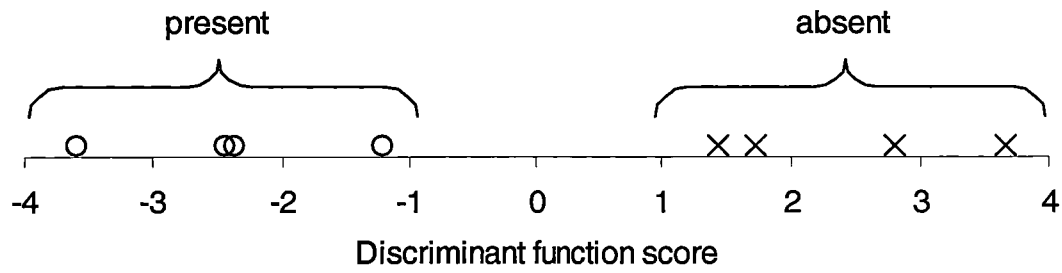

Figure 2.9 Distribution of discriminant function scores calculated for the four years where *Aurelia* sp. medusae were present (open circles) and the four years where medusae were absent (crosses).

CHAPTER 3:

POPULATION DYNAMICS AND AGGREGATORY MECHANISMS OF MOON JELLYFISH, *AURELIA* SP., MEDUSAE IN THE HUON ESTUARY, TASMANIA, AUSTRALIA

3.1 INTRODUCTION

Aurelia spp. are found in marine and estuarine environments around the globe. The distribution, abundance, and life history characteristics of this genus are highly variable both spatially and temporally (e.g. Yasuda 1970, Hernroth and Gröndahl 1985a, Purcell *et al.* 2000, Weisse and Gomoiu 2000). In most cases the pelagic medusae stage occurs seasonally and is short lived (e.g. Gröndahl 1988b, Lucas and Williams 1994, Miyake *et al.* 1997) but in some populations medusae have been found to live for 12 months or more (Yasuda 1971, Miyake *et al.* 1997).

The pelagic medusae stage begins with the release of juvenile medusae, called ephyrae, into the water column following their development by the benthic scyphistomae (e.g. Arai 1997). *Aurelia* medusae growth rates are rapid when in favourable conditions, however maturation and sexual reproduction will occur at a smaller size when growing conditions are less favourable (e.g. Schneider and Behrends 1994, Lucas 1996, Lucas *et al.* 1997, Båmstedt *et al.* 2001). *Aurelia* medusae are voracious feeders and when they occur in large numbers they are capable of modifying the seasonal composition and abundance of the planktonic community (Möller 1980b, Hernroth and Gröndahl 1983, Båmstedt *et al.* 1994, Behrends and Schneider 1995, Lucas *et al.* 1997). Secondary effects of high grazing pressure can include increased phytoplankton biomass through reduced grazing pressure by copepods (Möller 1980b, Lindahl and Hernroth 1983, Olsson *et al.* 1992), and decreased food availability for other zooplanktivores (Möller 1980b,

Purcell 1990). Jellyfish are also considered to be potentially important as consumers and transformers of energy and nutrients in the marine ecosystem (e.g. Purcell 1997, Olesen *et al.* 1994, Watanabe and Ishii 2001).

Aurelia medusae can concentrate into dense aggregations within enclosed or semi-enclosed water bodies (e.g. Papathanassiou *et al.* 1987, Hamner *et al.* 1994, Purcell *et al.* 2000, Colombo *et al.* 2003). Such aggregations are commonly believed to facilitate breeding (e.g. Yasuda 1971, Hamner and Jenssen 1974, Möller 1980a), rather than act as a defence against predation or targeting food sources (e.g. Matanoski *et al.* 2004). Formation of aggregations has been attributed to passive processes such as Langmuir circulation (Hamner and Schneider 1986, Larson 1992), convergences (Toyokawa *et al.* 1997, Purcell *et al.* 2000), wind, currents and tidal phenomena (Zavodnic 1987) as well as to behavioural processes such as diurnal vertical migration (Toyokawa *et al.* 1997), sun-compass migration (Hamner *et al.* 1994) and active maintenance of position within a salinity gradient (Toyokawa *et al.* 1997).

Aurelia sp. medusae occur in dense mono-specific aggregations in the Huon Estuary in south east Tasmania (Figure 3.1) in the summer of some years. The estuary is a strongly stratified micro-tidal salt wedge estuary with a relatively rapid flushing time of 2.5-6 days depending on local rainfall and subsequent river flow rates (CSIRO 2000). Medusae in the Huon Estuary are morphologically similar to *Aurelia aurita* (Spangenberg 1965) however they are genetically distinct from other populations of *Aurelia* (Dawson *et al.* 2005).

This study aims to identify patterns of growth and reproduction of the medusae, and mechanisms involved in aggregation formation and maintenance of this important component of the Huon Estuary ecosystem in a year of high medusae abundance. For the first time, estimates of aggregation size using aerial photography are combined with in-water measures of size, density and three-dimentional aggregation structure to provide estimates of the total number, and the total biomass of medusae within a system. Estimates of the daily increase in biomass of medusae and the daily ration requirements of the population in the Huon Estuary are also calculated. Reasons for the evolution of energetically expensive aggregatory behaviour are also discussed.

3.2 METHODS

3.2.1 Medusae Biology

Dense aggregations of *Aurelia* sp. medusae were found in Huon Estuary through December 2002 and January 2003. Aggregations were confined to a 10 km stretch of the estuary with individual medusae sparsely distributed outside this area (Figure 3.1). Medusae were collected from aggregations using a 40cm diameter 1mm mesh plankton net fitted with a General Oceanics flow meter. Oblique tows between 30 seconds and two minutes at a constant speed of 0.5-1.5 knots were made within aggregations from ~5m depth. The time of each tow depended on the density of medusae in each aggregation. Medusae were gently removed from the net and counted. A sub-sample of 20-30 animals was removed for examination in the field while still alive and a further 20-30

individuals were preserved in 4% formalin in seawater buffered with sodium borate for later assessment of maturity, fecundity, feeding status and diet composition (see below for details). All samples of medusae were collected from randomly selected aggregations, except on the 7th of January 2003 when three medusae were caught in a plankton net in the lower part of the estuary. These three individuals were included in the data used to model medusae growth, but were not included in any other analysis. All animals were collected in daylight hours between 0700h and 1600h.

The bell diameter (BD) of fresh, live medusae was measured by placing the individual upside down on a flat surface and measuring the distance between the tips of opposite rhopalia (marginal sense organs). The distance between the outer edges of each pair of opposite gonads (GD) was recorded as an additional measure of size for use in cases where bell margins were damaged. The relationship between GD and BD was represented by the equation:

$$GD = 0.4117BD - 9.8915 \ (n = 90, R^2 = 0.95)$$

Medusae were drained of excess liquid and wet weight (WW) was measured to the nearest gram. The relationship between WW and BD was represented by the equation:

$$WW = 01.12x10^{-4} * BD^{2.81} \ (n = 305, R^2 = 0.97)$$

Dry weight (DW) was calculated by first gently rinsing medusae in fresh water to remove salt, patting dry with paper towel to remove excess

water, and then weighing. Medusae were then dried to a constant weight in an oven at 50°C (Larson 1986) before being re-weighed. Dry weight was converted to carbon assuming 4.3% ±0.4 (se) of DW and to ash free dry weight (AFDW) assuming 21% ±0.3 (se) of dry weight (Larson 1986). It is recognised that the relationship between dry weight and carbon weight is affected by salinity (Larson 1986).

The amount of shrinkage (reduction in BD) during preservation was estimated by measuring BD and GD on fresh medusae before being stored in 4% formalin, and again after 22 weeks in the preservative. BD and GD were assumed to have stabilized by this time (Möller 1980a). The relationship between original size and size following preservation was represented by the equation:

$$BD_{(fresh)} = 1.22\ BD_{(preserved)}\ (n = 30, R^2 = 0.65)$$

where $BD_{(fresh)}$ = bell diameter of fresh medusa, and $BD_{(preserved)}$ = bell diameter of preserved medusa.

Medusae from each sample location were preserved and stored in large sealed drums. Preserved specimens were left for a minimum of 22 weeks before being examined and bell diameter was back calculated using the relationship derived from the shrinkage trial. 254 preserved specimens were measured for BD and GD.

The stomach contents of 100 preserved individuals from four different sampling days were examined. Individual stomach fullness was scored as 0 (empty), 1 (20% full), 2 (40% full), 3 (60% full), 4 (80% full), or 5 (full). The fullness of a stomach was the estimated proportion of the

stomach area containing prey when looking down at the dorsal surface of the medusae. Stomach fullness for individual medusae was the estimated average fullness of all four stomachs. The contents of each of the four stomachs in each medusa were gently removed from amongst the gastric filaments. Prey items were identified and enumerated to the level of major groups (Order and Family), and stage of development where appropriate (e.g. nauplii, megalopa etc), using a stereo dissecting microscope. Prey items were measured on their longest axis. This measure did not include flexible body parts such as legs and hairs but did include fixed and solid extensions of exoskeletons such as the rostrum. Prey items not readily identifiable at a magnification of 50X were not quantified and have not been included in this data set. Undigested hard parts of prey (exoskeletons) identified in stomach contents were also excluded from the data set. Medusae were grouped into two size classes (small <100mm and large >100) based on the median bell diameter of the medusae examined, and time of capture was classified as morning, midday or afternoon. Differences in frequency distributions of stomach fullness among time of capture and prey size between large and small medusae were tested using χ^2 tests of independence.

Sex and maturity stage was determined as:

1) juvenile (J; gonad thin, clear, indistinguishable as male or female);
2) immature male (IM; gonad clear/opaque, follicles where spermatogenesis takes place beginning to form in the epithelium);
3) mature male (MM; gonad dark pink/purple, follicles well developed);

4) immature female (IF; gonad clear/opaque, developing oocytes visible, large late stage oocytes few or absent);

5) mature female (MF; gonad opaque pink/purple, many large late stage oocytes); and

6) brooding female (BF; gonad as for MF and with fertilised eggs and planula larvae present in brood pouches on oral arms).

Gonads from 39 mature and brooding females were removed and examined using a dissecting microscope. The diameter of a random selection of approximately 100 oocytes was measured from each female using transmitted light at 50X magnification and a graticule eyepiece. Females were grouped by BD (50-100mm, 101-150mm, 151-200mm) and by sample day. Differences in oocyte size frequency distributions between groups of different BD were tested using χ^2 tests of independence. Expected values were generated on the assumption that oocyte frequency distribution and body size distribution are independent of each other.

Zooplankton biomass in the Huon Estuary was calculated by collecting plankton samples at three locations: H1, H3, and H12 (Figure 3.1) every 4-6 weeks from March 2001 to March 2003 and every 1-3 weeks when medusae were abundant. Samples were collected using 65cm ring diameter bongo nets fitted with General Oceanics flowmeters. One side of the bongo frame was fitted with a 500μm mesh net and the other side was fitted with a 315μm mesh net. To standardise samples, plankton tows were oblique from 10m to the surface and at a constant speed of 2-3 knots for three minutes at each location. Samples were

rinsed with distilled water using filter paper over a vacuum before being dried to a constant weight at 70°C.

3.2.2 Aggregation Dynamics

Movement and structure of aggregations in the Huon Estuary were observed on seven separate days between the 15th and the 24th of January 2003. A small boat equipped with a GPS mapping system, echo sounder, and underwater camera was used to locate and determine the size, shape, and pattern of vertical distribution of 10 separate aggregations. On two occasions SCUBA diving was also used to confirm camera and echo sounder observations, as well as to gain a more detailed understanding of the three-dimensional shapes of individual aggregations. Individual aggregations were observed over several hours during which time the location of the centre point of the aggregation was repeatedly estimated and recorded with the GPS mapping system providing estimates of subdaily scale movement of aggregations within the estuary. An acoustic doppler current profiler (ADCP) was deployed adjacent (across current) to four different aggregations on separate occasions at a distance of no more than 100m. It was assumed that the current direction and velocity profile information measured at this distance from an aggregation was the same as that experienced by the aggregation. The ADCP split the water column into 10 equal sized depth bins and calculated the average current velocity and direction for each depth bin approximately every seven minutes during a deployment. These data were stored internally until the instrument was retrieved. ADCP data were analysed to identify and characterise different components of the water column, and calculate net

movement of the whole water column. A YSI 6600 multi-function probe equipped with temperature and salinity meters and a data logger was used to determine the presence of temperature or salinity gradients associated with boundaries of aggregations of *Aurelia* sp. medusae.

3.2.3 Population Structure

An aerial survey of aggregations of *Aurelia* sp. in the Huon Estuary and adjacent waters was made during the afternoon of the 23rd of January 2003. A single engine light plane with three observers, flying at an altitude between 1000 and 5000 feet was able to cover the area comprehensively and identify all visible aggregations in a 60 minute flight (method modified from Purcell *et al.* 2000). Ground truthing on the day using a small boat equipped with an underwater camera established that aggregations observed from the air comprised of *Aurelia* sp. medusae. A random search of the estuary using the echo sounder and underwater camera was made to determine if any aggregations were present that were not visible from the air. Low oblique photographs were taken of each aggregation with care taken to include as many geographical features in the field of view as possible (e.g. points, bays, boat ramps, fish farms, roads and houses). Images were geo-rectified (Wolf and Dewitt 2000) to fit a scale map of the Huon Estuary and aggregation outlines were digitised and the surface area calculated. The depth of water at the location of each aggregation was determined from bathymetric charts and the vertical distribution of aggregations was estimated based on the 'typical' pattern observed in aggregations in the Huon Estuary during the 2002/03 summer (3.2.2 Agregation Dynamics).

The number of individuals in each aggregation and the total biomass of the estuary was calculated using the mean density of medusae measured in four aggregations on the day of aerial photography as well as the day before and the day following. There was no relationship between aggregation size and the density of medusae within aggregations, however it must be noted that the "typical" vertical distribution patterns and mean density can only really be applied to the size range of aggregations tested and as such do not necessarily cover those aggregations which were smaller and only observed from the air.

3.2.4 Statistical Methods

Growth rate of medusae was modeled by fitting a curve to BD data for the period of bell growth. Measurements of BD from the last two days (30th and 31st January; Day 56 and 57) showed a break down in the growth pattern. These animals were dying and drifting down the estuary near the surface and were treated as a single sample. These data were not included in the growth model. Samples were pooled into four time periods:

1) 5/12/2002-29/12/2002;

2) 29/12/2002-19/01/2003;

3) 19/01/2003-24/01/2003; and

4) 24/01/2003-31/01/2003

Mean daily growth rate was calculated for each period on the basis of increments in BD:

$$\text{growth} = (W_2/W_1)/(t_2 - t_1)$$

where W_1 and W_2 are the mean bell diameters of each period, and t_2 and t_1 are the day numbers of two consecutive periods. A logistic model of proportional maturity at length using maximum likelihood estimation assuming a binomial error distribution (Deriso and Quinn, 1999) was fitted to the data to determine the size at which 50% (s50) and 95% (s95) of male and female medusae were mature.

3.3 RESULTS

3.3.1 Medusae Biology

Aurelia sp. medusae were found in large dense aggregations in the Huon Estuary in south east Tasmania during the summer of 2002/03. Medusae were first collected on the 5th of December 2002 (Day 1) in an aggregation at Killala Bay (Figure 3.1) and had a mean bell diameter (BD) of 19.0mm ±1.4 (se). There was only evidence of a single cohort in the population throughout the season. Medusae grew exponentially from early December through to late January 2003 (Day 50). This was followed by a short period (seven days) where no further growth occurred prior to medusae disappearing from the estuary at the end of January (Day 57) (Figure 3.3). During this period the physical condition of all medusae observed deteriorated with the marginal region disintegrating. Maximum growth rates of 4.99mm or 7.3% DW day^{-1} were recorded in the period ending where maximum size was recorded in the Huon Estuary (Table 3.1). Dry weight of medusae in the Huon Estuary was 3.7% of wet weight. During the period of maximum growth, mean sized medusae were gaining dry weight at a rate of 464.89 mg day^{-1} and carbon at 20 mg

day^{-1} (Table 3.1). BD increased by approximately 420% in one month up until the pattern of growth broke down after Day 50. Maximum mean size was reached on the 24th of January (Day 50) at 156.8mm ±4.4 (se). The largest medusa, which was sampled on 24th January, was 246mm.

Distinct peaks in zooplankton biomass were evident over six week periods in both summers covered by sampling. The zooplankton bloom in 2002/03 occurred approximately 1 month earlier than in 2001/02, and peak biomass values were approximately 25% lower at 40mg m^{-3} in 2002/03 than in the previous year. Biomass was low and relatively steady at 3-6mg m^{-3} during the remainder of each year outside the bloom periods. The timing of the appearance of medusae in the estuary, the timing of maximum daily growth and maximum size, and the timing of medusae growth breaking down and medusae disappearing from the estuary appeared to track zooplankton biomass with a lag period of 5-10 days (Figure 3.4).

Individual medusa of maximum mean size (BD = 156.8mm) were calculated to consume between 45.2mg and 361.4mg AFDW of prey per day based on the daily ration range of 5%-40% of medusa AFDW (Båmstedt 1990). The same size medusa would require a daily maintenance ration of at least 90.4mg based on Båmstedt's (1990) conservative estimate of 10% of body AFDW (Table 3.2).

Stomach fullness of medusa was dependant on time of day ($\chi^2 = 42.83$, df 10, $P < 0.001$) with animals captured earlier in the day having less food in their stomachs than animals caught later in the day (Figure 3.5). The number of prey items in a medusa ranged from 0-183,

with an average number of 30.2 ±3.8 (se). Seventeen taxonomic groups were identified in the stomachs of medusae caught across all periods. Numerically, gastropods formed the major component of stomach contents followed by calenoid copepods, amphipods, brachyuran zoea and porcelenid zoea (Table 3.3). Fish larvae and fish eggs were not a significant component of the stomach contents of medusae, with only one fish larva and eight eggs found in a total of 2717 prey items from 100 individual medusae.

The number of prey items in stomachs was dependant on medusa size ($\chi^2 = 18.59$, df 4, $P = 0.001$) with small medusa (<100mm BD) having fewer prey items than large medusa (≥100mm BD) (Figure 3.6). Prey size was also correlated with medusa size with both the average and maximum size of prey items found in stomachs tending to increase with BD (Figure 3.7 (a & b)). The largest prey item was a porcellenid crab zoea which was 21.7mm long measured from the tip of the posterior carapace spine to the tip of the rostral spine (Figure 3.7 (b)). The average size of prey items found in *Aurelia* sp. stomachs was 1.8mm. There was no relationship between medusae size and the smallest prey items (that was resolved under the microscope) found in stomachs indicating that medusae retain the ability to capture small prey items as they grow while gaining the ability to handle larger prey items (Figure 3.7 (c)).

Fifty percent of female *Aurelia* sp. medusae reached maturity at 101mm BD and 95% at 125.6mm. Fifty percent of males reached maturity at 90mm BD and 95% at 131mm (Figure 3.8). Maturity was not as tightly constrained by size in males as it was in females with a larger

difference in BD between 50% maturity and 95% maturity. The minimum size at maturity in 2003/04 was 76mm for females and 60mm for males (Figure 3.8). The largest immature animal sampled was a 113mm BD female.

The maturity status of females in the aggregations changed significantly over the intensive part of the sampling period ($\chi^2 = 28.03$, df 5, $P < 0.001$), with the proportion of mature females in the population increasing with time (Figure 3.9 (a)). Samples from the early part of the season (5th December and 7th January) were not used in this analysis as all medusae were juvenile and sex was indeterminate. The sex of medusae was determinable from the 7th of January and the first mature medusae were seen on the 19th of January. Seventy eight percent of males and 65% of females were mature by the 19th of January. The number of immature animals reduced over the remainder of the season with 100% of males and 89% of females mature on the 30th January. There was a general increase in the proportion of females carrying planula larvae (BF) as the season progressed, however there was substantial temporal variation (Figure 3.9 (a)). There was a reduction in the number of immature males from 100% to 22% from the 7th January to the 19th January and to zero by the end of the season (30th of January) (Figure 3.9 (b)). The sex ratio over the summer was approximately 1:1 although there was some fluctuation between samples during the season (Figure 3.10). The proportion of males had fallen to 25% on the last sample of the season.

The size frequency distribution of oocytes in the gonads among medusae size classes (BD; 50-100mm, 101-150mm, 151-200mm) was different ($\chi^2 = 28.8$, df 12, $P = 0.004$), with large animals (151-200mm) tending to have larger, mature oocytes. There were also significant differences in the size frequency distribution through time (medusae grouped by sample date; 19/01, 20/01, 22/01, 24/01, 30/01) ($\chi^2 = 140.8$, df 24, $P < 0.001$) with mature female gonads containing more small oocytes than expected early in the season and more large mature oocytes than expected later in the season (Figure 3.11). This pattern was not continued in the last sample of the season however, where medusae collected were in poor condition and the large discrete aggregations previously sampled were not able to be located despite extensive boat based visual and acoustic searches. Mature oocytes were 170-210μm in diameter with no oocytes larger than 210μm found. The distribution of oocyte size in the gonads was predominantly skewed with a large number of small, immature oocytes present. No discrete peaks were evident in the size frequency distributions and the smooth tapering tail towards the upper end of the size distribution indicates that *Aurelia* sp. medusae were trickle spawning rather than batch or single spawning.

3.3.2 Aggregation Dynamics

Aggregations generally had very sharp, planar boundaries (±1-2m) on all sides including the top and bottom. The tops of aggregations were readily visible from the surface and were usually 1-3m below the surface regardless of surface or water column conditions. Aggregations appeared to be a uniform density right through the water column as shown by

underwater camera and diver observations, however density was not measured at discreet locations within aggregations to confirm this. The bottom boundaries of aggregations were parallel to the sea floor and were usually 1-3m above the bottom. Edge boundaries were usually vertical but were sometimes distorted with bulges and ridges extending horizontally out from aggregations for up to 5m. Often the depth sounder gave aggregations the appearance of being hollow in the centre, similar to *Aurelia aurita* aggregations described by Toyokawa *et al.* (1997), but a camera lowered through the aggregations showed a distribution that appeared uniform throughout. These aggregations were usually very dense when viewed from the surface and it is suggested that the poor 'reflective' quality of the middle part of the aggregation (hollowness) was an artefact of the density of medusae through the upper part of the water column interfering with reflections from layers below giving an incorrect 'picture' of aggregation structure. When the three-dimentional underwater shapes of an aggregations were not measured they were assumed to extend vertically downwards from the visible surface 'footprint' shape, to 1.5m above the bottom. The average density of aggregations over the sampling period ranged from 18-270m^{-3} with an average of 133 individuals m^{-3} ±37.2 (se). There was no correlation between aggregation size and density (Pearson's r = 0.098, P = 0.80).

Water movement in the water column was not uniform in direction or velocity. In four of the five sampling periods where aggregations were being monitored concurrently with water movement, the water column could be split into two clearly identifiable layers. On each occasion the

upper 8-10m of the water column was moving in a north to north-westerly direction while the lower part of the water column was flowing in a south-westerly to south easterly direction. The current velocity in any depth bin ranged between 7-105mm sec^{-1} with an average depth bin velocity of 42mm sec^{-1} ±1.1 (se). Aggregations maintained their high density and discreet structure over many hours despite spanning two separate layers in the water column moving in different directions. The observed direction and velocity of movement of whole aggregations within the estuary closely approximated the net direction and velocity calculated for the whole water column.

Coordinated swimming of medusae was observed visually from the surface, by SCUBA diver, or with underwater cameras. This behaviour was observed in all aggregations however coordination was not uniform throughout individual aggregations. Medusae in any one area of an aggregation were observed swimming uniformly in one direction while medusae in other parts of the same aggregation would all be uniformly swimming in other directions. On some occasions there was no visible coordinated swimming behaviour visible in the surface layer of aggregations while at other times nearly 100% of individuals would be swimming horizontally in a uniform direction. On other occasions all medusae in the centre area of the surface of an aggregation would be swimming downward yet the surface of the aggregation did not get any deeper indicating possible localised upwelling events which may have been bio-convection cells generated by the aggregations themselves.

Observations of medusae on the vertical side boundaries of two aggregations, on the 19th and 22nd of January, revealed a complex and coordinated behavioural pattern which potentially contributed to maintenance of the tightly aggregated form. A diver descending down the outer edge of one side of aggregation number one observed that all individuals were swimming straight down the outer edge from the surface of the aggregation at 2m down to 8m. Below this was a section of medusae that were all swimming straight up from 10m to 8m and meeting those coming down from above. No collisions or disruption to the swimming pattern of individuals was observed above or below this meeting point suggesting that medusae turned inward at this point and swam toward the centre of the aggregation, although this could not be observed from outside the aggregation. At 10m there was a narrow band of low density below which all medusae were swimming vertically down to the bottom of the aggregation at 14m. At this point the medusae turned and disappeared under the bottom of the aggregation (Figure 3.12). Observations of the outer edge of one side of aggregation number two showed that all medusae near the outer edge of the top of the aggregation (2m) were swimming horizontally toward that edge before turning and swimming down to 4m. There was a narrow band of uncoordinated swimming at 4m where approximately 50% of medusae were swimming up and 50% were swimming down. From 4m down to 10m all medusae were again observed swimming straight down. The uncoordinated swimming observed at 4m may have been due to the meeting of two distinct circulation cells within the aggregation. At 13m

there was another band of confused swimming where medusae swimming down from 4m met with animals swimming up from 13m. Again, no collisions or disruption to the swimming pattern of individuals was observed above or below this meeting point suggesting that medusae turned inward at this point and swam toward the centre of the aggregation. Below 13 m there was a 1-2m band of lower density where all medusae were swimming horizontally out from under the aggregation (Figure 3.12).

3.3.3 Population Structure

A total of 22 aggregations were identified in the lower Huon Estuary during an aerial photography flight on the 23rd January. These aggregations were a pale green colour and were clearly visible from the air (Plate 3.1). Aggregations ranged in shape from circular to elliptical although one aggregation photographed was very long and narrow measuring 300m by 30m. It was assumed that all aggregations present in the estuary and its extensions were visible at the surface at the time of the flight based on the fact that all aggregations of *Aurelia* sp. detected in the Huon Estuary over the summer, using visual and acoustic methods and plankton nets, extended to within a few meters of the surface and were clearly visible from the boat at all times during the day.

The mean density of medusae in aggregations was estimated to be $71m^{-3}$ ±32.7 (se) based on density measurements two days either side of the day of the aerial survey (23rd January). It was assumed that this density estimate reflects the mean density of medusae in aggregations observed in the Huon Estuary on the day of the aerial photography. It

was also assumed that the pattern of vertical distribution of medusae through the water column on the day of the aerial survey followed the same patterns observed over the summer using echo sounder, underwater camera, and diver observations.

The largest aggregation observed during the summer had a volume over 600 000m^3 and contained an estimated 100 million individuals. The largest aggregation on the day of the aerial photography was estimated to be a little over a third of this size at 233 000 m^3 and contained an estimated 23 million medusae. The smallest aggregation measured on any day was 5 200m^3 estimated from an aerial photograph and contained in the order of 370 thousand individuals. The mean estimated volume of aggregations on the day of the aerial photography was 112 000 cubic meters containing around 7.9 million medusae (±1.4 million) (Table 3.4). The total number of medusae in aggregations in the Huon Estuary on the 23rd January was estimated to be 169 million with a DW of 1058t and incorporating 45t of carbon (Table 3.5).

Using a DW to AFDW conversion of 21% (Larson 1986) and the estimates of daily ration and maintenance ration requirements (4-40% of body weight and 10% respectively) (Båmstedt 1990) it was estimated that an average size aggregation consumed between 0.5 and 4.2t (AFDW) of food day^{-1} and have required 1.1t day^{-1} for the individuals within the aggregation to maintain body size. The whole population would have consumed in the range of 11.1-90.8t (AFDW) day^{-1} and required 22.7t day^{-1} to maintain body size (Table 3.2).

3.4 DISCUSSION

3.4.1 Medusae Biology

The occurrence of *Aurelia* sp. medusae in south east Tasmania follows an annual cycle with recruitment and slow growth of small medusae in early spring followed by exponential growth over the summer period. Towards the end of the 2002/03 summer the medusae population in the Huon Estuary went through a short period where the pattern of growth broke down and the condition of medusae deteriorated. Within 10 days of peak medusae size and growth rates, the large aggregations that had been present until that time could no longer be found, and no medusae at all were found after this time. The observed pattern of growth may have been due to a real cessation of growth of individuals in the population at this time. Alternately, it may have been a result of Lee's Phenomenon which occurs when individuals are still growing but where the larger individuals in the population are senescing and disappearing from the population faster than smaller animals. Exactly which process was operating in the Huon Estuary at the time can not be determined with these results, however, given the degenerating condition of the vast majority of individual medusae at the time it is thought that growth had ceased and the population as a whole was collapsing.

The exponential pattern of growth of medusae followed by a population crash has also been observed in other populations (e.g. Hamner and Jenssen 1974, Schneider 1989, Olesen *et al.* 1994, Miyake *et al.* 1997, Uye and Shimaughi 2005), although there are considerable

variations in life history characteristics between populations. The population in the Huon Estuary is similar to those in Southampton Water (Lucas and Williams 1994) and Tomales Bay (Hamner and Jenssen 1974) that occur at the same time of the year and have similar patterns of growth. Other populations have the same growth patterns but appear prior to winter and persist well into autumn (e.g. Möller 1980a, b, Schneider and Behrends 1994, Miyake *et al.* 1997), or have multiple cohorts and are present in the water column year round (Yasuda 1971, Lucas 1996, Miyake *et al.* 1997).

Both the number of prey items and the mean and maximum size of prey items increased with medusae size. Prey capture rates in *Aurelia aurita* medusae increase with bell size (Båmstedt 1990). The mechanisms for this increase include increased prey capture area (Larson 1986, Lucas 2001), increased area of water 'searched' with each bell pulsation (Bailey and Batty 1983, Costello and Colin 1994), and the generation of stronger bell margin currents allowing capture of prey items with faster escape responses (Costello and Colin 1994). In addition larger medusae may have an increased ability to handle and process larger prey items due to the presence of physically larger prey handling structures including oral arms and gastro-vascular apertures.

Sufficient food availability is critical to sustaining the exponential growth pattern of animals observed in the Huon Estuary. In the Huon Estuary medusae size increase corresponded with the pattern of zooplankton biomass and around 5–10 days following the peak in zooplankton a peak in medusae growth was observed. The pattern of

growth (and shrinkage) of *A. aurita* has a similar close link to food availability (Olesen *et al.* 1994, Lucas *et al.* 1997). It is likely that the observed reduction in zooplankton biomass resulted in a reduction in food availability for medusae in the Huon Estuary and therefore a reduction in growth rate. Sufficient information was not available to determine whether the decline in zooplankton biomass seen in the Huon Estuary was caused by predation pressure from the medusae. However, dense populations of scyphozoans are capable of reducing zooplankton biomass (e.g. Omori *et al.* 1995, Lucas *et al.* 1997, Schneider and Behrends 1994), and a decrease in growth rate after a high initial rate is often the result of changes in the environment induced by the organisms themselves (Coyne 1973).

The pattern of growth of medusae in the Huon Estuary broke down to the extent that mean size began to decrease at a rate of 1.5% day^{-1}. Reduction in size of medusae is a common component of *A. aurita* biology with medusae able to survive through periods of low food availability by utilising resources held in body tissues (Hamner and Jenssen 1974). Negative growth rates of 18% in the month following sexual reproduction (0.6% day^{-1}) (Möller 1980a) and up to 70% reduction in size after 100d of starvation (Hamner and Jenssen 1974) have been observed. It has also been suggested that slowing of growth of *A. aurita* in summer is not due to food limitation but rather to a shift of energy allocation from somatic growth to reproduction (Hansson 1997), however this study showed that a large proportion of both males and females were already fully mature prior to any reduction in growth rates occurring.

The reason for the rapid deterioration of the physical condition of the medusae and their subsequent disappearance from the estuary is unclear. Population crashes are a common component of scyphozoan biology (e.g. Möller 1980a, Lucas and Williams 1994, Ishii *et al.* 1995), with theories including, senescence of medusae after spawning (Spangenberg 1965, Lucas 2001), infection with the parasitic amphipod *Hyperia galba* (Rasmussen 1973, Gröndahl 1988b), and genetic determination (Hamner and Jenssen 1974). There was no evidence of 'spent' female gonads at the end of the season, with 89% of females with mature oocytes present in the gonads making it doubtful that medusae were senescing following spawning. Similarly, there was no evidence of an influx of any sort of obvious parasites toward the end of the season, however it is possible that a microscopic parasite or a disease may have amplified within the population causing the observed decline. The death of animals with remaining reproductive potential is common among short-lived species with indeterminate life spans (Stearns 1992) and the presence of medusae with mature oocytes and planula larvae at the time of the population declining indicates that senescence was not genetically pre-determined.

Medusae were found to have progressively more food in their stomachs through the day suggesting medusae fed throughout the day with a reduction in predation rates over night during which time digestion rates outstripped ingestion rates and stomach fullness reduced. This conflicts with the idea that zooplankton are more active and therefore more available in the water column during the night. Medusae

living in the surface layers (0-20m) of the water column over much deeper waters (20-120m) do take advantage of increased zooplankton food availability occurring *in surface waters* at night (Vereshchaka 2002). However, as aggregations of *Aurelia* sp. were observed to extended from near the surface to near the bottom, and large scale movements of individuals within those aggregations was observed, it was assumed that zooplankton prey, accept for those species that are closely associated with the benthos, would be accessible to all medusa*e* throughout the 24 hour period.

Feeding in *A. aurita* is a function of the rate of pulsing of the bell as well as food availability (Bailey and Batty 1983). The lower stomach fullness indices of *Aurelia* sp. observed early in the day may have been due to reduced swimming activity at night resulting in fewer prey captures relative to the day when increased swimming activity would result in more captures. This contrasts with evidence suggesting medusae swimming rates are correlated with surface illumination with higher rates of bell pulsing during periods of illumination (Mackie *et al.* 1981), however medusae behaviour was not examined outside daylight hours in this study. Although the distribution of *Aurelia* sp. medusae was not observed during the hours of darkness, they were in tight aggregations extending from near the surface to near the bottom from at least sunrise to sunset. The presence of dense, discreet aggregations at dawn suggests that medusae remained active at night to maintain aggregation integrity, although the level of activity, and therefore predation, may have been reduced from that observed during the day.

Medusae in the Huon Estuary had an average of 30.2 ±3.8 (se) prey items in their stomachs when captured. This was far less than calculations of individual consumption of 100's to 1000's of prey items per day in Prince William Sound (Purcell 2003), however with estimates of digestion times for small copepods of between 0.95h (Ishii and Tanaka 2001) and 0.71h (Dawson and Martin (2001) in *A. aurita* and around 3h in *Aurelia labiata* (Purcell 2003). It is unlikely that the contents of the stomach represents more than a small portion of the daily ration and with these digestion times taken into account, the estimated daily consumption for *Aurelia* sp. falls in the mid to high 100's and is comparable with literature values.

The diet of *Aurelia* sp. medusae consisted predominantly of gastropods, copepods, amphipods and crab zoea. This study showed fish eggs and fish larvae were unimportant in the diet of *Aurelia* sp., despite November to February being the peak period of fish egg and fish larvae abundance in the region (Cheshuck 2001). In some cases gelatinous zooplanktivores have been shown to be important consumers of fish eggs and larvae (Shushkina and Musayeva 1983, Bailey and Batty 1983, Möller 1984, Shiganova and Bulgacova 2000) while other studies have found them to make up only a small percentage of the diet of gelatinous predators (Purcell 2003, Barz and Hirche 2005). Some prey selectivity is likely to occur as a function of escape response velocity of prey (Costello and Colin 1994), and post capture selection of particles (Stoecker *et al.* 1987). Food particles smaller than those easily identifiable at 50X

magnification were not examined here, however phytoplankton is not utilized as a food source by large medusae (Båmstedt 1990).

3.4.2 Aggregation Dynamics

Aurelia sp. medusae were grouped together into discreet, dense aggregations in the Huon Estuary. Most medusae present in the system were either within, or closely associated with one of these aggregations. Anecdotal evidence (pers. comm. Atlantic salmon aquaculture industry) suggests that similar extreme patchiness was evident in previous years of high *Aurelia* sp. abundance. Advantages of being in an aggregation can include increased feeding, improved reproductive success, protection from predation, and improved ability to remain within a suitable physical environment (Matanoski *et al.* 2004). Similar aggregations of *Aurelia* spp medusae have been reported (Yasuda 1970, Hernroth and Gröndahl 1985a, Papathanassiou *et al.* 1987, Hamner *et al.* 1994, Toyokawa *et al.* 1997, Purcell *et al.* 2000), however little information is available concerning the mechanisms involved in their formation and maintenance, and the information that is available is often conflicting.

The majority of the literature concerning aggregations suggests that medusae are either aggregated by passive mechanisms including broad-scale oceanographic processes creating frontal features of various types (Mutlu 2001), and fine scale circulation features such as tidal current sheer, wind driven circulation including Langmuir circulation cells, and various frontal features (Haury 1978, Hamner and Shneider 1986), or by active (behavioural) mechanisms in response to physical cues. Examples of active aggregation include diurnal migration (Yasuda

1974, Mackie *et al.* 1981, Hamner *et al.* 1982), sun-compass migration (Hamner *et al.* 1994) and active maintenance of position within salinity, temperature and pH tolerances (Miyake *et al.* 1997, Toyokawa *et al.* 1997).

This study was unable to detect any physical hydrographic features commonly associated with passive aggregatory mechanisms, with either the formation, or the maintenance of aggregations in the Huon Estuary, although the specialised equipment necessary to detect current sheer along a vertical plane in the water column was not used. However, a highly complex pattern of active, coordinated movement of many medusae throughout aggregations was observed in the Huon Estuary. Medusae are able to react behaviourally to unknown physical cues in the water column (Purcell *et al.* 2000). These cues may facilitate aggregation formation and maintenance and could include some unknown chemical marker associated with individuals in an aggregation, physical contact with other medusae, recognition of reaching the 'edge' boundary of an aggregation, and detection of circulation cells (bio-convection) within aggregations generated by the behaviour of individuals in the aggregation itself (Purcell *et al.* 2000).

Scyphozoans are not generally considered capable of extensive movements against currents (Graham *et al.* 2001). However, discreet *Aurelia* sp. aggregations in the Huon Estuary were observed to persist for at least 14 hours during the day despite the presence of strong opposing current layers. The complex pattern of movement of individuals observed within aggregations were difficult to rationalise, however the possibility

that aggregations contained a number of isolated circulation cells within which medusae were able to continually move promoting aggregation maintenance rather than decay (Purcell *et al.* 2000) is possible. Elsewhere coordinated swimming of scyphozoans also contributes to aggregation formation and maintenance (e.g. Hamner *et al.* 1994, Purcell *et al.* 2000, Dawson *et al.* 2001b). Medusae have been shown to be able to detect and orientate themselves to currents *in situ* and in aquaria (Hamner and Schneider 1986, Shanks and Graham 1987) therefore 'bio-convection' within aggregations may play an important role in promoting the persistence of aggregations, particularly in the presence of the strong two-layer circulation pattern present in the Huon Estuary. The lack of evidence of purposeful movement of aggregations suggests that the coordinated activity of individuals may be more important for aggregation maintenance rather than for maintenance of position within the estuary, or any deliberate movement of aggregations toward more desirable locations such as areas of higher prey abundance.

The maintenance of aggregations must involve a heavy energetic expense. *Aurelia* sp. are dioecious therefore spawning must occur in close proximity to other medusae of the opposite sex for fertilisation to be successful. It is likely that the formation and maintenance of aggregations is necessary to facilitate reproductive success as well as helping with maintenance of position within an environment like the Huon Estuary with relatively strong currents and short flushing times.

3.4.3 Population Structure

Estimates of density and biomass of medusae have been made in the past using the more traditional method of plankton nets filtering known volumes of water and expressing results as units per m^{-3} (e.g. Lucas 1996, Lucas *et al.* 1997). This method would not provide valid results for the extreme patchiness observed in the Huon Estuary. The approach of using aerial surveys to quantify the number of medusae in a waterway has been used before (e.g. Purcell *et al.* 2000). These methods are useful for making comparisons of medusae abundance within any given water body between years, however they are unable to provide valuable quantitative biological information for inclusion in ecosystem modelling.

Impacts of large *Aurelia* sp. biomass on the Huon Estuary ecosystem are unknown at this time, however, heavy predation by the large biomass of medusae observed in the Huon Estuary could significantly reduce the zooplankton standing stock (Purcell 1997, 2003), induce phytoplankton blooms by reducing grazing pressure (e.g. Olsson *et al.* 1992, Purcell 1997, Brouder *et al.* 2002), increase competition for food resources with other zooplanktivores including fish larvae (Möller 1980a), and modify the flow of energy and nutrients through the local ecosystem (e.g. Olesen *et al.* 1994, Ishii and Tanaka 2001, Uye and Shimaughi 2005). The methods developed in this study have successfully provided abundance and biomass estimates for the Huon Estuary that will be valuable for assessing potential impacts of jellyfish blooms in the region as well as forming an important component in ecosystem models used to assess the effects of Atlantic salmon aquaculture operations in the region.

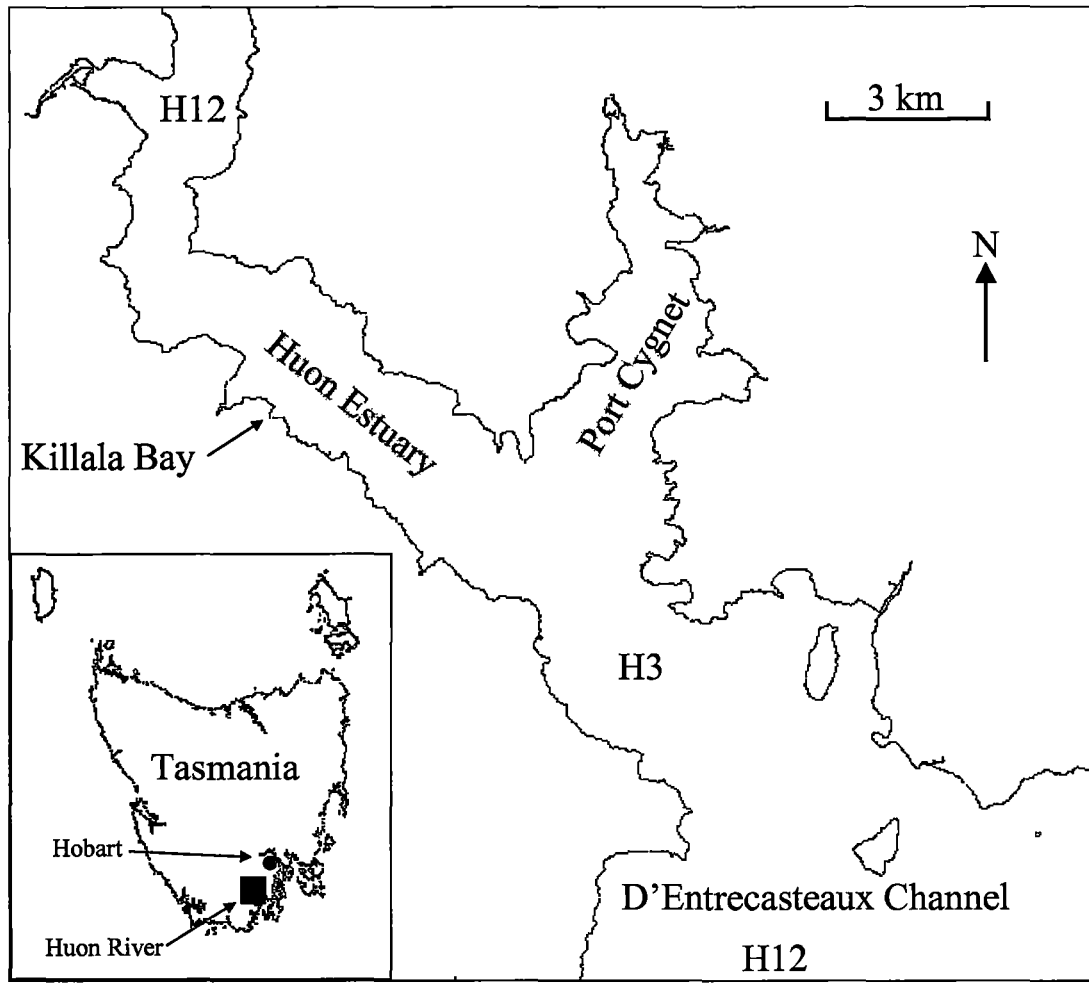

Figure 3.1 Location of the Huon Estuary in south east Tasmania, Australia. The stippled area shows the section of the estuary where aggregations were observed during the summer of 2002/03.

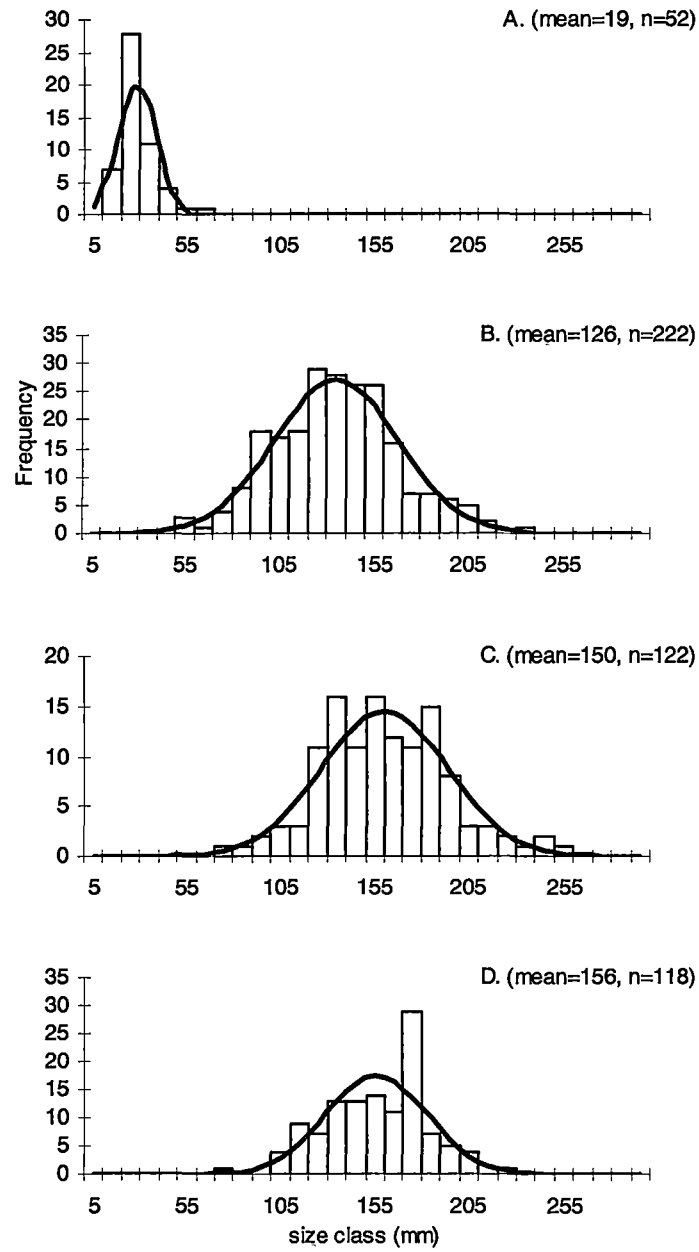

Figure 3.2 Bell diameter frequency distributions for Aurelia sp. medusae collected in the Huon Estuary during four sample periods in the summer of 2002/2003; a) 5/12/02 – 6/12/02, b) 15/01/03 – 19/01/03, c) 20/01/03 – 24/01/03, and d) 30/01/02 – 31/01/02.

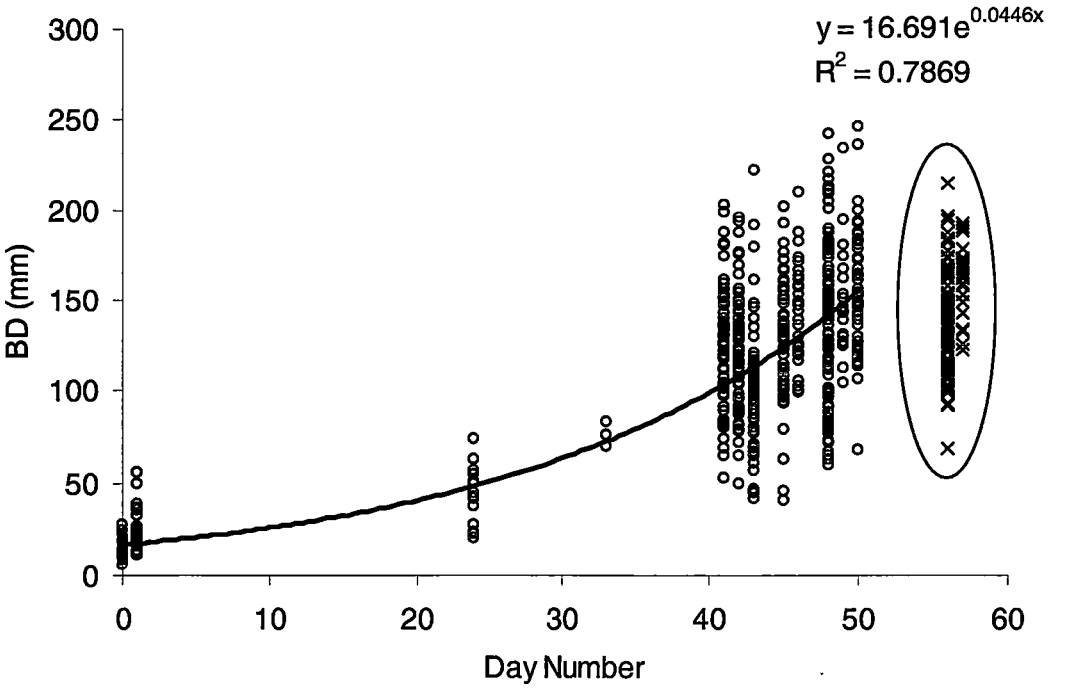

Figure 3.3 Bell Diameter (BD) of *Aurelia* sp. in the Huon Estuary from 5th December 2002 (Day 0) to 31st January 2003 (Day 57) n = 645. The model is fitted to data up to Day 50 (open circles), but does not include later data where population decline was occurring (crosses). The circled data are from medusae collected after growth had stopped and were not included in the model.

Table 3.1 Summary of mean medusae size and mean medusae growth rate for each sample period.

Sample Period	Mean Bell Diameter	n	Growth (day-1)					
			BD (mm)	Wet Weight (g)	Dry Weight (mg)	AFDW (mg)	Carbon (mg)	% Weight Increase
5/12/2002 (medusae first observed)	18.99	52						
5/12/02-9/12/02	43.50	14	1.07	0.2	8.9	1.9	0.4	3.7
29/12/02-19/01/03	125.51	222	4.10	5	185	38.9	8	4.7
19/01/03-24/01/03	150.48	122	4.99	12.6	464.9	97.6	20	7.3
24/01/03-31/01/03	146.41	118	-0.51	-2.3	83.9	-17.6	-3.6	-1.5

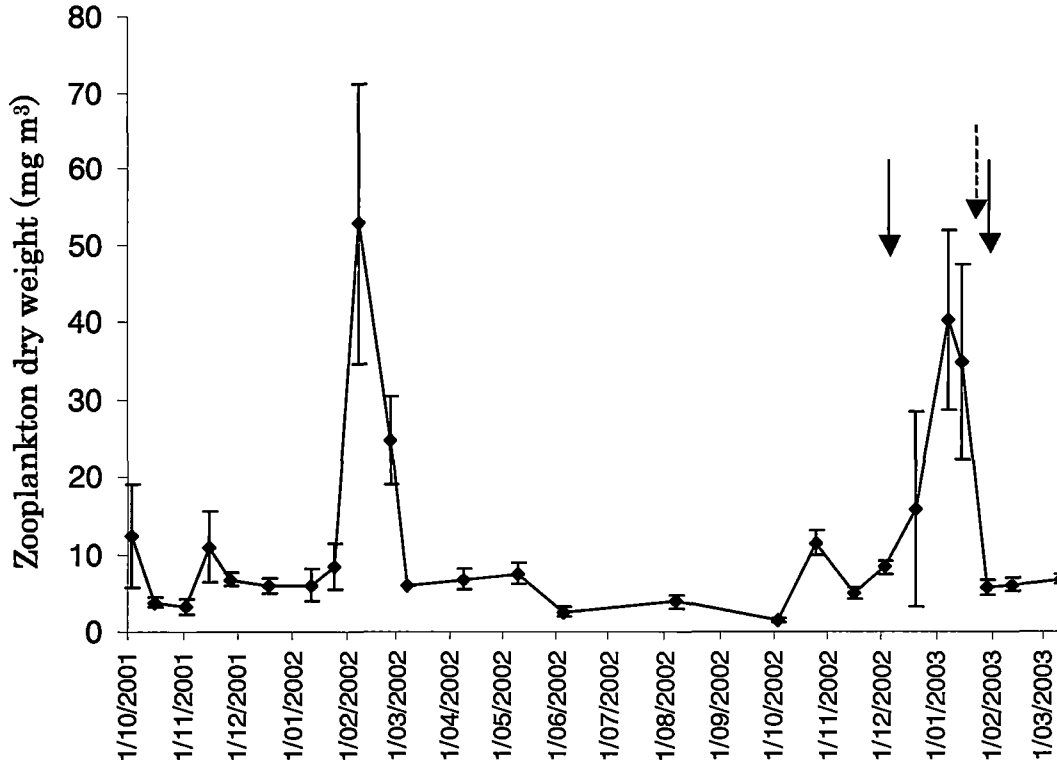

Figure 3.4 Zooplankton dry weight biomass measured in the Huon Estuary from March 2001 to March 2003. The solid arrows indicate the timing of the *Aurelia* sp. medusae bloom in the Huon Estuary, from the time the medusae were first observed at the start of December 2002, to their disappearance at the end of January in 2003. The dashed arrow indicates the timing of maximum mean bell diameter, and peak biomass of medusae. Note that although there was a corresponding peak in zooplankton biomass the preceding year (February 2002), the peak occurred one month later in summer and no medusae bloom occurred in that summer.

Table 3.2 Predicted daily ration for large medusae (BD = 156.8mm) in the Huon Estuary on 23rd January 2003. Weights are AFDW of prey items.

	Minimum Ration (5%)	Maximum Ration (40%)	Maintenance Ration (10%)
Per Individual (mg)	67.2	537.6	134.4
Per Aggregation (t)	0.5	4.2	1.1
Whole Population (t)	11.1	90.8	22.7

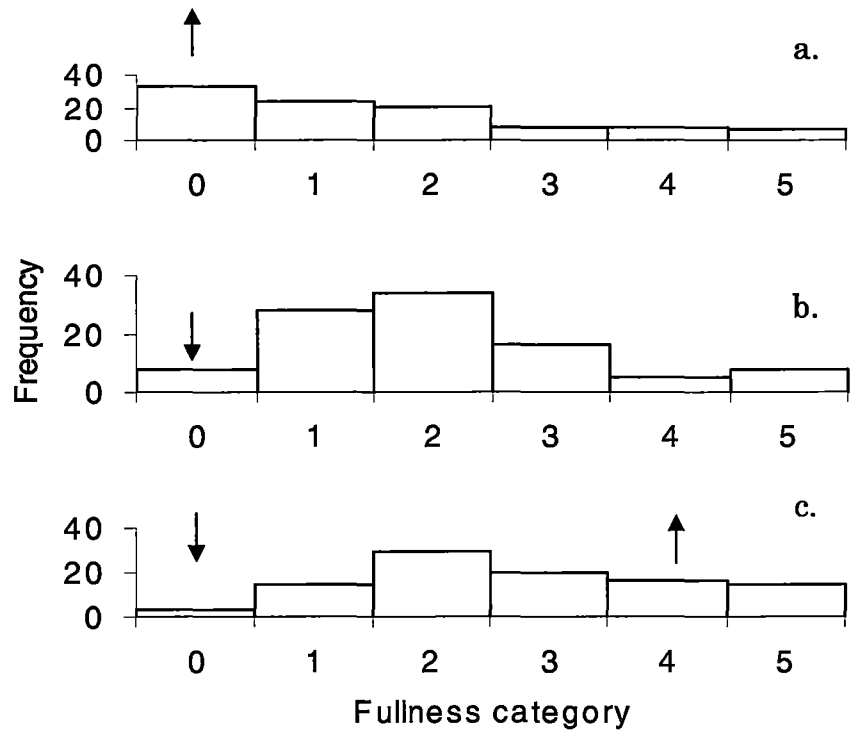

Figure 3.5 Frequency distributions of stomach fullness category (0 = empty, 5 = Full) for medusae caught at three different periods during the day; a) morning, b) middle of day, c) afternoon. Arrows indicate where and which direction the observed results depart from expected.

Table 3.3 Mean number and type of prey items in stomachs of individual *Aurelia* sp. medusae from the Huon Estuary in 2002/03, ordered from most to least common prey items.

Taxanomic Group	% Occurrence
Gastropods	47.23
Calenoid Copepods	29.31
Amphipod	14.20
Brachyuran crab zoea	3.10
Porcelinid crab coea	2.10
Bivalve moluscs	1.77
Ostracod	0.48
Anomura/Caridea zoea	0.37
Bryazoan larvae	0.33
Fish Egg	0.29
Brachyuran crab megalopa	0.18
Barnacle nauplii	0.11
unidentified	0.11
Barnacle cypris	0.04
Lucifer	0.04
Shrimp	0.04
Fish larvae	0.04
Mysid shrimp	0.04

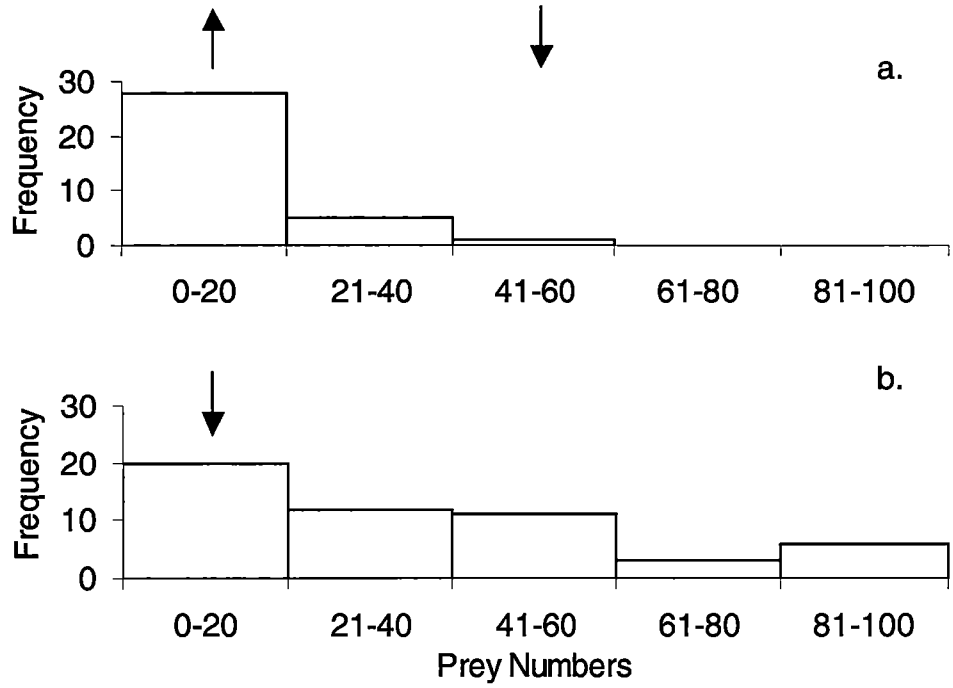

Figure 3.6 Frequency distribution of the number of prey items in stomachs of medusa from two size classes; a) BD <100mm, b) BD ≥100mm. Arrows indicate where and in which direction observed frequencies depart from expected.

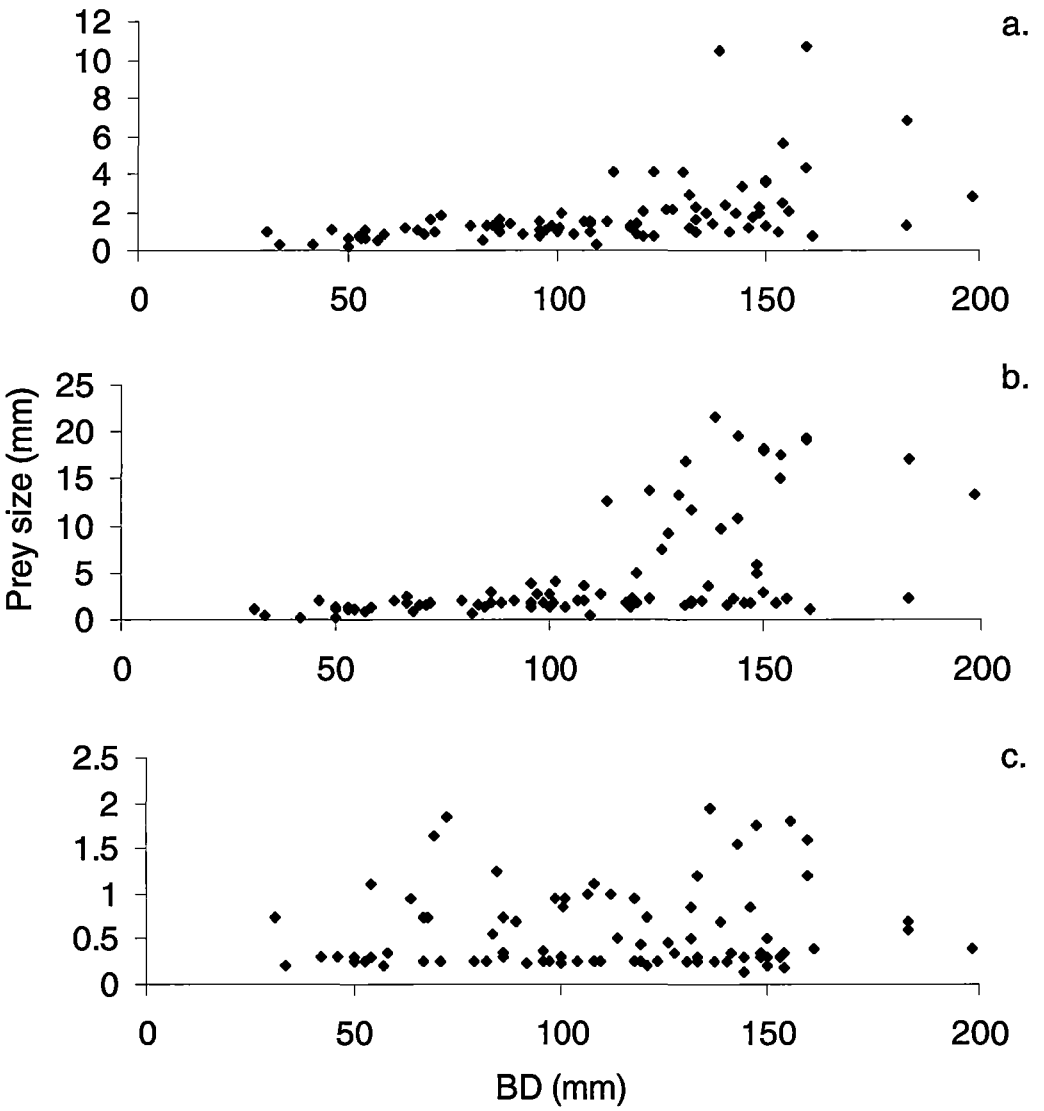

Figure 3.7 Relationship between bell diameter and; a) average size, b) maximum size and c) minimum size of prey items in stomach contents of medusae from the Huon Estuary 2002/03.

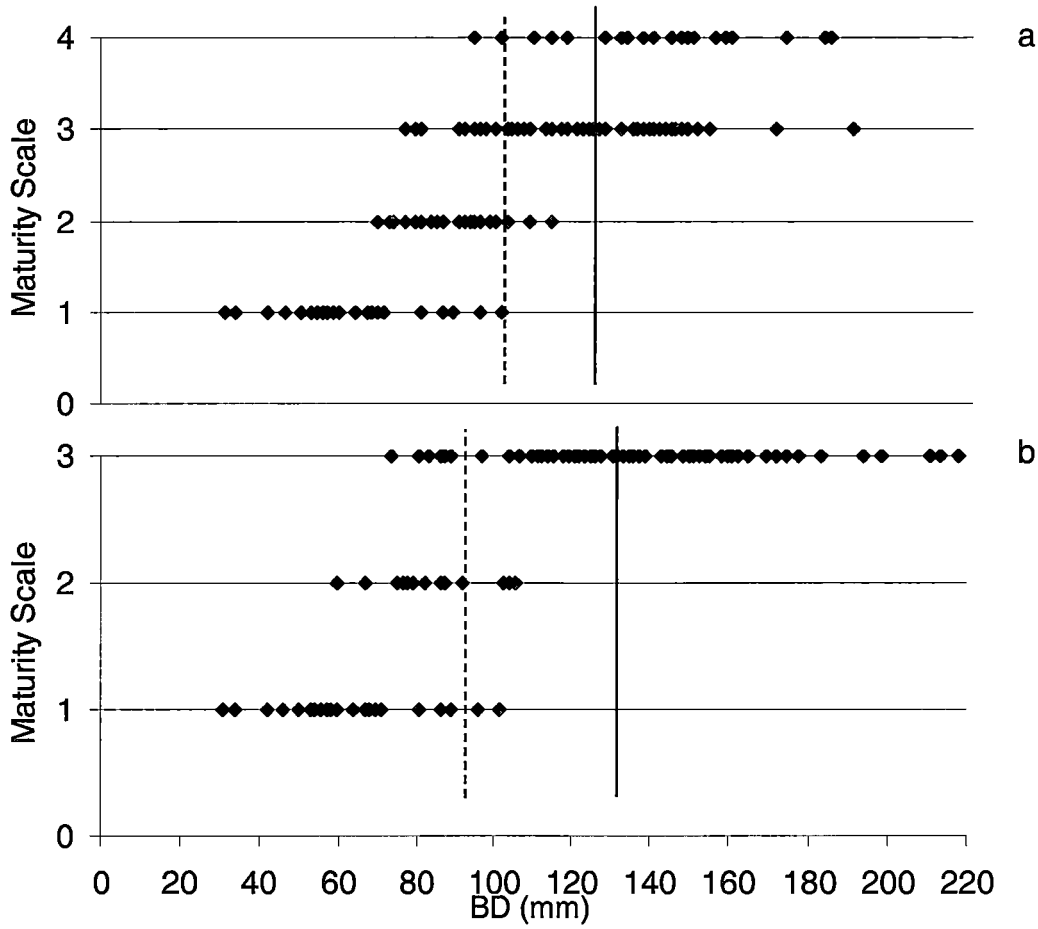

Figure 3.8 Maturity ranking and Bell Diameter for: a) Female (n = 148) and b) Male (n = 134) *Aurelia* sp. medusae (1-juvenile, 2-immature, 3-mature, 4-females carrying planula larvae). Dashed lines show the size at which 50% of medusae were mature, solid lines show the size at which 95% of medusae were mature.

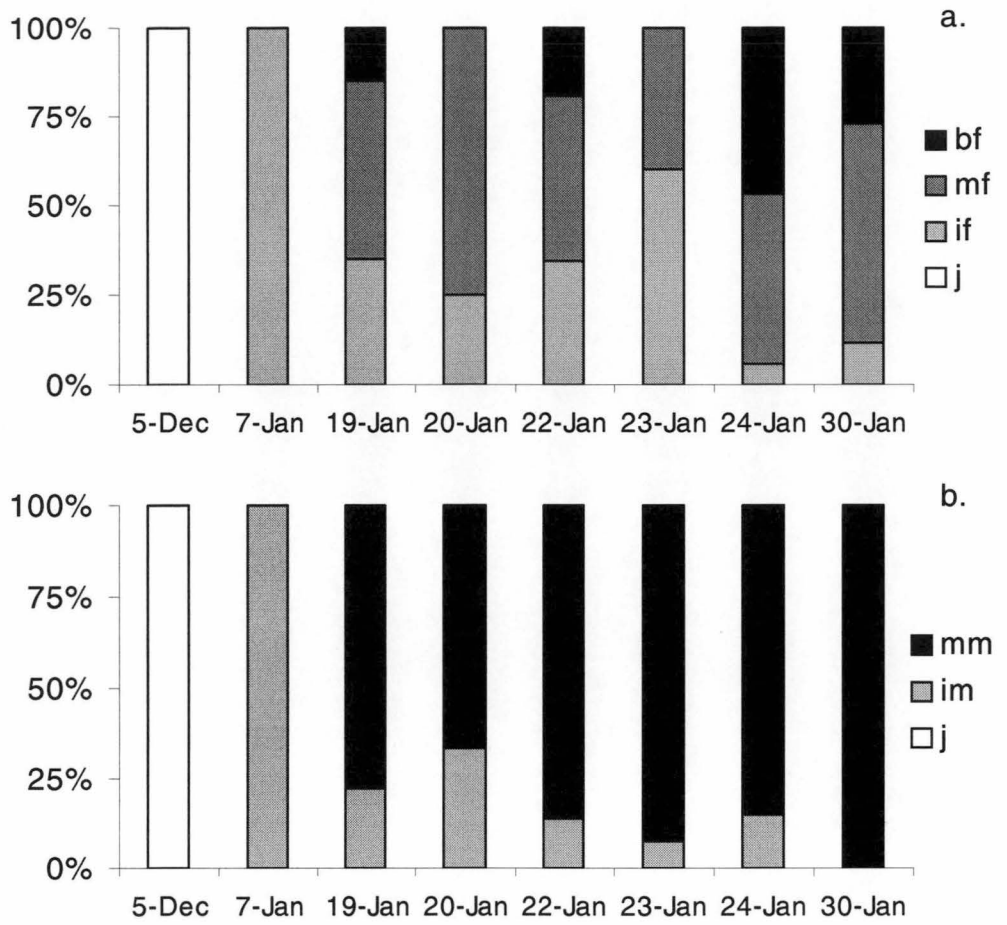

Figure 3.9 Maturity status composition of the *Aurelia* sp. population on each sample day for: a) Female medusae (j = juvenile, if = immature female, mf = mature female, bf = brooding female), and b) Male medusae (j = juvenile, im = immature male, mm = mature male) in the Huon Estuary in the 2002/03 summer.

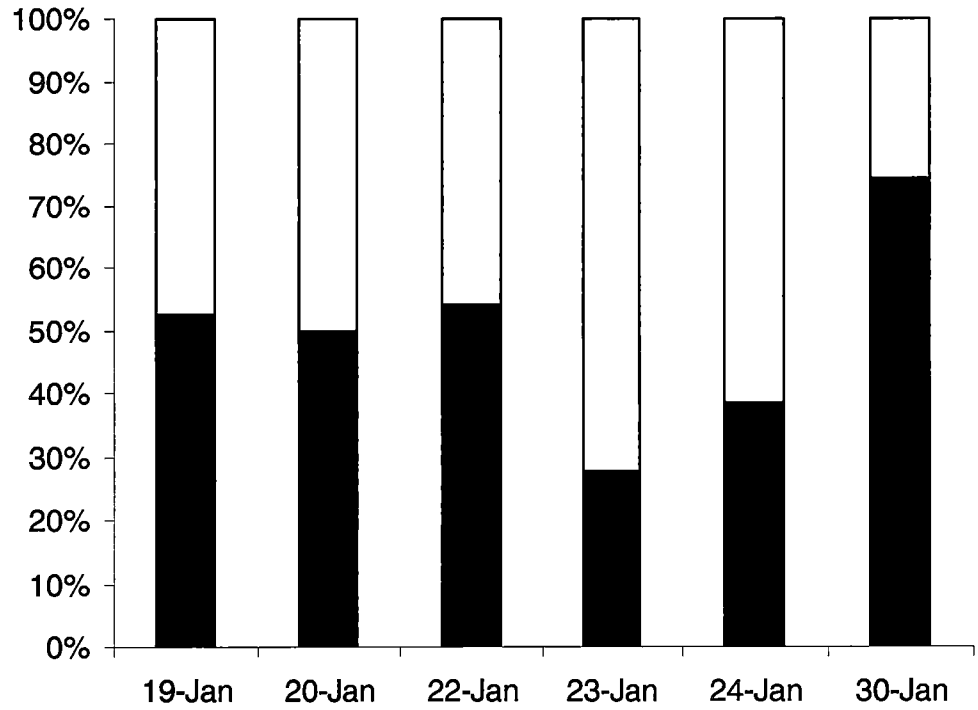

Figure 3.10 Sex ratio of *Aurelia* sp. medusae in the Huon Estuary in January 2003 (black = female, white = male).

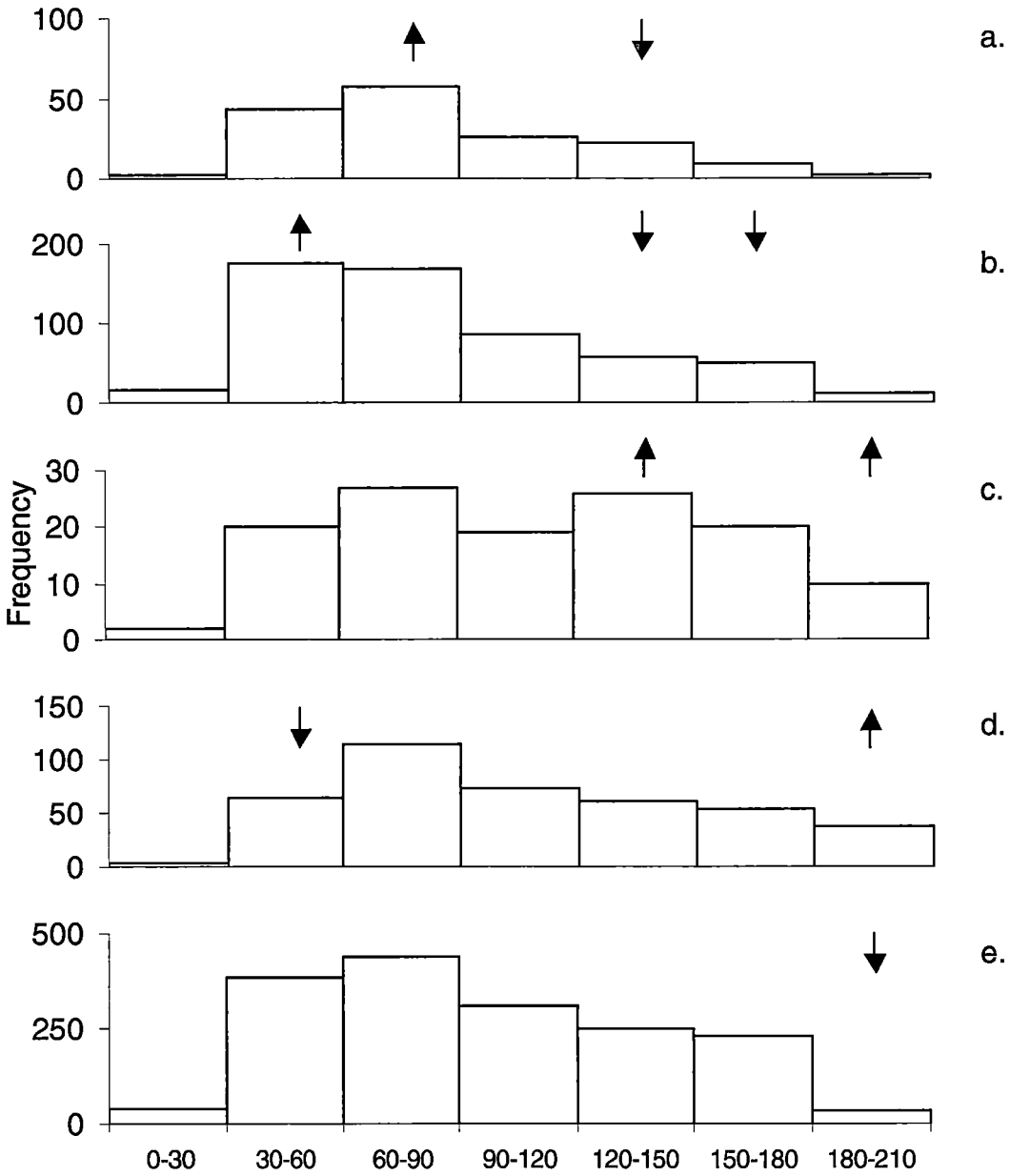

Figure 3.11 Oocyte size frequency distribution for mature medusae from the Huon Estuary, January 2003 grouped by sample date. a) = 19th January (n = 163), b) = 20th January (n = 565), c) = 22nd January (n = 124), d) = 24th January (n = 410), e) = 30th January (n = 1688). Arrows indicate where and in which direction the observed frequencies departed from expected.

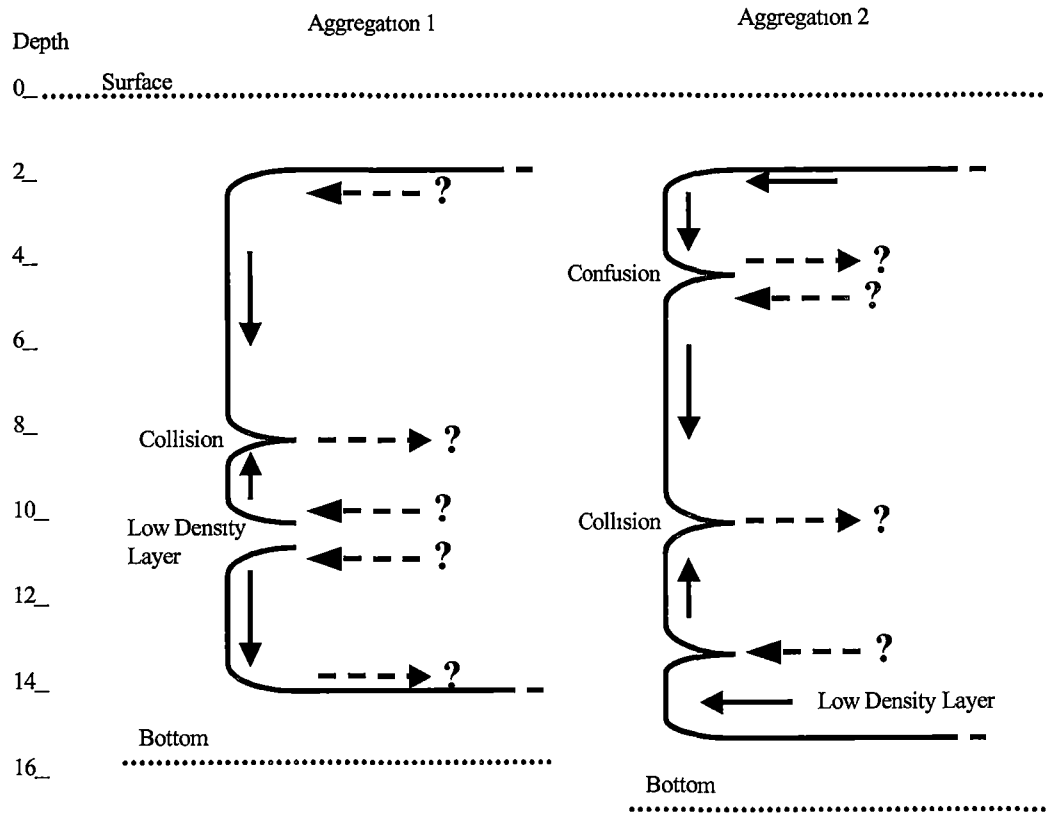

Figure 3.12 Schematic diagram detailing observed medusae orientation and coordinated swimming direction in two aggregations observed by SCUBA diver in the Huon Estuary. Solid lines define the edge of the aggregation, solid arrows indicate observed orientation and direction of swimming of medusae, dashed arrows with question marks indicate suggested direction of movement of medusae inside the aggregations which might explain observed external behaviour.

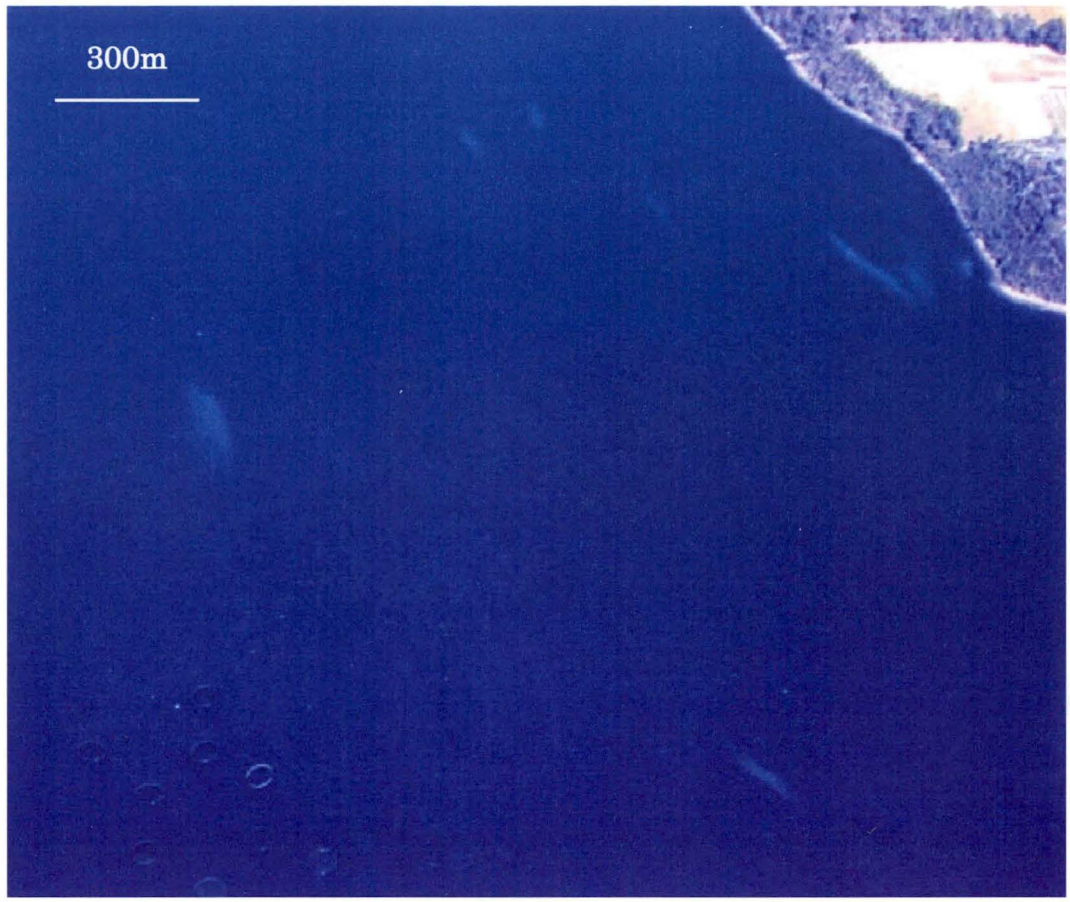

Plate 3.1 Low oblique aerial photograph of aggregations of *Aurelia* sp. medusae in the Huon Estuary, south east Tasmania, in January 2003. Aggregations appear as light patches in the water and are highly visible from the air. Note the close proximity to Atlantic salmon aquaculture cages in bottom left of photograph.

Table 3.4 Mean aggregation size and mean number of medusae in aggregations in the Huon Estuary on 23rd January 2003 estimated from aerial photographs.

	Mean	n	SE
Mean aggregation volume (m^3)	111 668	22	21 397
Assumed mean density (individuals m^{-3})	71	4	32.7
Mean number of medusae per aggregation (millions)	7.9	22	1.4

Table 3.5 Total number of medusae, biomass and total weight of carbon held in medusae tissue in the Huon Estuary on the 23/01/2003 estimated from aerial photographs.

	Estimated values
Total number of medusae	169 million
Wet weight biomass	28 600 tons
Dry weight biomass	1 058 tons
Ash Free Dry Weight	222 tons
Total carbon	45 tons

CHAPTER 4:

POPULATION DYNAMICS OF *AURELIA* SP. SCYPHISTOMAE IN SOUTH EAST TASMANIA, AUSTRALIA

4.1 INTRODUCTION

The mechanisms driving blooms of jellyfish in coastal waters and the reasons for large year to year variability in jellyfish abundance have received much attention in recent literature (e.g. Möller 1980a, Papathanassiou *et al.* 1987, Omori *et al.* 1995, Brodeur *et al.* 2002). Juvenile pelagic stages (ephyra) of many jellyfish species develop from asexual benthic scyphistomae, therefore the abundance and distribution of the scyphistomae can have a direct impact on the distribution and abundance of the bloom forming medusae stage (Brewer and Feingold 1991, Watanabe and Ishii 2001, Colin and Kremer 2002). Potential factors which can influence scyphistomae abundance include: recruitment of larvae to the substrate (Lucas 2001); predation (Hernroth and Gröndahl 1985b, Keen 1991, Osman and Whitlatch 2004); competition for space (Coyne 1973, Watanabe and Ishii 2001); competition for food (Harper 1985); food availability (Hernroth and Gröndahl 1985a, Keen and Gong 1989, Purcell *et al.* 1999a); cannibalism (Kikinger 1992); water temperature (Omori *et al.* 1995, Purcell *et al.* 1999b, Miyake *et al.* 2002) and salinity (Purcell *et al.* 1999b).

The benthic phase is an important component of the life cycle for several reasons. It is perennial and enables populations to survive through years when recruitment to the short-lived sexual phase fails and it provides the opportunity to greatly increase the population size in preparation for production of the dispersive ephyrae when conditions are suitable (Keen 1991). The ability of scyphistomae to reproduce, compete, and survive increases with colony size and understanding processes

involved in colony growth are important for understanding life history strategies in scyphozoans (Garrabou 1999).

The ability to produce many individuals asexually allows clonal animals to both disperse, and occupy space more rapidly and efficiently than aclonal species (Gong 2001). By producing many small individuals, clonal organisms can grow free from morphological and physiological restraints faced by aclonal organisms such as maximum size, senescence, and surface area to volume ratios. They also have some of the advantages of larger animals such as greater food capture ability and protection from predation, as well as some of the advantages of smaller animals, such as not being limited by spaces where they can physically fit (Marfenin 1997). While food and space are not limiting, clonal animals are able to potentially increase their population size indefinitely (Gong 2001) enabling them to establish a numerically large base from which to produce the dispersive pelagic stage when conditions are favourable.

Scyphistomae of *Aurelia* spp. are found on the underside of hard substrata (e.g. floating pontoons, buoys, bare rock, algae, and encrusting organisms including oysters, mussels and ascidians (Brewer 1978, Gröndahl 1988b, Miyake *et al.* 2002), and at densities of 60-400 thousand individuals m^{-2} (Gröndahl 1988b). Once the planktonic planula larvae from the sexual medusae stage settle onto a suitable substrate they metamorphose into scyphistomae and begin reproducing asexually by budding. During budding outgrowths develop on the body walls of the parent. Each outgrowth develops into a fully functional scyphistoma before being released. Individual scyphistoma can have up to nine buds

developing at one time (Spangenberg 1964b). When environmental conditions are favourable, budding exceeds mortality and population size can increase rapidly (Lucas 2001). Ephyrae are produced by scyphistomae in a second mode of asexual reproduction called strobilation and are released into the plankton when they are fully developed (Arai 1997). Temporal observations of scyphistomae colonies and ephyrae abundance in the plankton show strobilation usually takes place during a short and well coordinated period of 1-3 months in winter/early spring when water temperatures are lowest (e.g. Lucas 1996, Miyake *et al.* 2002). However, timing of strobilation can vary and has been observed occurring over a seven month period (Lucas 1996), in two separate periods within one year (Hernroth and Gröndahl 1983, 1985a), and continuously throughout the year (Spangenberg 1964a). When a scyphistoma has finished strobilating it resumes feeding and budding and it may strobilate several times in its lifespan (Gong 2001).

Factors influencing the distribution, abundance, and survival of the scyphistomae are key to understanding the distribution and abundance of the medusae (Colin and Kremer, 2002). Studies examining factors involved in regulating population size and rates of asexual reproduction in the scyphistomae are summarised in Table 4.1. The rate and timing of asexual reproduction in the scyphistomae is dependant on the environmental conditions in which they find themselves (e.g. Hughes and Cancino 1985, Purcell *et al.* 1999b). However, the population dynamics of the benthic phase of the life cycle, and links with environmental conditions, remain poorly understood (Purcell *et al.* 1999b, Lucas 2001).

Most of what is known about scyphistomae population dynamics is based on laboratory experiments (e.g. Spangenberg 1965, 1968, Coyne 1973, Kakinuma 1975). Few *in situ* studies of this small and cryptic stage have been conducted, and of those, most have been restricted to examination of settling plates (e.g. Hernroth and Gröndahl 1983, 1985a, Watanabe and Ishii 2001, Miyake *et al.* 2002).

This study aims to examine spatial and temporal patterns in the population dynamics of naturally occurring colonies of *Aurelia* sp. scyphistomae in south east Tasmania to identify potential environmental controls of the two modes of asexual reproduction, and of mortality. The use of artificial substrates deployed at each colony site allowed the study of colony dynamics *in situ* but in conditions where density dependant effects were reduced from those operating in adjacent naturally occurring colonies. This gave a clearer understanding of environmental controls over colony size, as well as an understanding of how rapidly new habitats might be colonised in south east Tasmania, whether they be natural substrates previously unoccupied by scyphistomae or new man-made structures introduced to this environment. Finally, the importance of several key environmental parameters in controlling rates and timing of reproductive processes are discussed in relation to the life history strategy of this ecologically important scyphozoan.

4.2 METHODS

Population dynamics of naturally occurring colonies of *Aurelia* sp. scyphistomae were monitored at two sites in south east Tasmania from

October 2002 to December 2004. One site was in the Derwent Estuary, Hobart (Figure 4.1), located on the underside of a rigid cement breakwater at a depth of approximately 2.5m ± calm tidal excursions. The second site was at Kettering in the D'Entrecasteaux Channel approximately 30km south of Hobart (Figure 4.1) and was located on the underside of a floating marina at a depth of 0.5 m. Both sites were low energy environments, sheltered from swell surge and tidal flows. Colonies were restricted to the horizontal underside of the structures with no scyphistomae present on the vertical sidewalls of either the breakwater or the floating marina.

Fifteen haphazardly placed 0.09m^2 photo-quadrates were taken at each site approximately every six weeks (Plate 4.1) using a five mega pixel digital camera in an underwater housing operated by a SCUBA diver. The camera was fitted with a framing arm that ensured the camera was perpendicular to and the same distance from the substrate for all photographs. The camera settings for focal length and zoom were the same on each sampling day ensuring the area and scale of photographs was the same each day. Errors in area measurements due to optical distortion characteristics of the camera and underwater housing lenses were quantified by photographing a grid of known dimensions underwater and calculating the size of each grid square using image analysis software. A mean area estimate error of 2.2% ±0.4% (se) was calculated. This level of error was accepted and no calibration was used prior to image analysis. The distribution of scyphistomae on colony

substrates was patchy. Patch size ranged from a few cm^2 to >>$0.09m^2$ (maximum size of images).

Six artificial substrates consisting of 15cm x 15cm x 3mm black acrylic plates were attached at each site to study the process of colonising bare substrate. Plates were lightly abraded with steel wool to roughen the surface and remove any contaminants before being attached to the colony substrate (cement breakwater or cement pontoon) using 'Z-Spar' 2-pack epoxy putty. Care was taken to make sure the edges of plates were flush with the substrate ensuring continuity of the surface from natural to artificial. Plates were allowed to 'acclimatise' for six weeks before being wiped clean of all biofouling organisms using steel wool. Each plate was then photo-sampled at six week intervals over three consecutive 18 week periods. Each plate was wiped clean of all biofouling organisms including scyphistomae at the end of each 18 week period. This regime of sampling and cleaning facilitated the study of colony growth during three distinct periods of the year; January-May (summer/autumn), May-August (winter) and August-December (spring). For the purposes of this study the substrate where scyphistomae colonies were found naturally is referred to as 'natural' substrate, and the acrylic plates are referred to as 'artificial' substrates.

Images were analysed using Sigma Scan Pro 5. image analysis software. From each photograph the areas of non-strobilating scyphistomae, strobilating scyphistomae, bare substrate, algae, other, and obscure categories was determined (Table 4.2). The area occupied by each category was digitised and the total area calculated for each image.

Density was measured in two ways. 'Patch density' refers to the number of scyphistomae in a patch divided by the area covered by that patch, while 'population density' refers to the number of scyphistomae within the photographic field of view divided by the area of the photograph.

Patch density was estimated on each sampling occasion by counting the number of scyphistomae within grid squares of known area superimposed over scyphistomae patches in each image. Population density was estimated from patch density and the percentage cover of scyphistomae on each sampling occasion. The distance that scyphistomae had incurred onto plates at subsequent samples following cleaning (encroachment) was the shortest perpendicular measurement from a plate edge to the scyphistoma attached closest to the centre of that plate.

Water temperature was not different between colony sites during a trial period in summer ($F = 0.1$, df 1,7, $P = 0.8$) and temperature was subsequently recorded at Kettering only. Temperature was recorded four hourly using an Onset Optic Stowaway temperature data logger that remained *in situ* from May 2003 to December 2004. The data logger was downloaded periodically throughout the deployment period.

Salinity was measured at the depth of the colony on four occasions at each site using a WTW salinity meter. Three samples were on randomly selected dates. The fourth sample targeted the end of a three day period of very heavy rainfall to confirm that rainfall was having an effect on salinity at colony sites, as well as to determine how low salinity might get at colony sites. Daily rainfall, recorded by the Bureau of Meteorology at Margate, was used as a proxy for salinity when examining

temporal changes in colony dynamics. Rainfall was assumed to have an immediate and short term impact on salinity based on the measurements of salinity during and after rainfall, as well observations throughout the study where sampling following rainfall resulted in poorer image quality from discoloured water.

4.2.1 Statistical analysis

Three-way ANOVAs were used to examine the effect of year, colony site and season on the proportion of the substrate occupied by scyphistomae, patch density and population density. Season was identified by water temperature, with the warmest period of each year being 'summer' and the coolest period being 'winter'. Periods of increasing or decreasing water temperatures in between were defined as 'spring' and 'autumn' respectively. A 'year' was the 12 month period from the start of one summer period to the start of the next summer period. Tukeys HSD post hoc tests were used to determine differences among means when ANOVAs were significant.

Temporal patterns in scyphistomae density and substrate coverage were explored using multiple regression. Water temperature, rainfall, and the area of bare substrate were tested as predictor variables for density. Mean water temperature and rainfall values for the 30 day period prior to each sample day were used in regression analysis. Data were grouped by year allowing interannual differences in relationships between predictor variables and dependent variables to be examined.

Univariate repeated measures ANOVAs were used to examine the effects of site and season on the rate of encroachment of scyphistomae, changes in the proportion of the substrate covered by scyphistomae, and changes in scyphistomae density on artificial substrates. Pairwise comparisons were made using repeated measures ANOVA to compare rates of change between sites and among seasons where significant effects of site and/or season were found. The Type II error rate was adjusted for the number of tests, to $\alpha = 0.006$.

Heterogeneity of variance was checked using residual plots. Population density was transformed (log 10) for analysis and the results were back-transformed for graphical presentation.

Interaction terms were tested for all analyses and where significant, this term was explored using the tests outlined above and presented graphically. Where the interaction term was not significant the main effects were explored using the tests outlined above and presented graphically.

4.3 RESULTS

4.3.1 Environmental parameters

Water temperature during the study was 7.7-20.4°C. Mean water temperature during the periods when artificial substrate experiments were conducted was: summer/autumn; 16.2°C, winter; 10.4°C, and spring; 13.4°C.

Salinity was typically 31-34‰, however salinity dropped suddenly during heavy rainfall and subsequent runoff. The Hobart site was

particularly susceptible to short term fluctuations in salinity due to large influxes of fresh water from a nearby stormwater outfall as well as from the Derwent River. Here the lowest salinity at the depth of the colony was measured at 27.3‰ following heavy rainfall. The same rainfall event resulted in a salinity of 30.7‰ at the Kettering colony.

4.3.2 Dynamics of naturally occurring colonies

Percent cover

There was a three-way interaction (Year*Site*Season) in the percent cover of the substrate occupied by scyphistomae ($F = 3.4$, df 3, 238, $P = 0.018$). Percent cover at Kettering was consistently higher than at Hobart with Kettering having a mean cover 1.5-6 times greater than Hobart (Figure 4.2). The percent cover of scyphistomae did not change at Kettering during the two year study, however there were large seasonal differences at Hobart (Figure 4.2). The highest cover of scyphistomae (56%) at Hobart occurred in summer 2003. There was a significant decline in percent cover through autumn and into winter 2003 when mean cover had decreased to nine percent before increasing again through spring and into summer 2004 (Figure 4.2). Although the pattern of high cover in summer and low cover in winter appeared to be repeated in 2004, variability was high and no differences were evident among seasons in that year. Percent cover at Hobart did not reach the level of the previous summer (2003) for the remainder of the monitoring period, with a maximum mean cover of only 32% recorded the following summer (Figure 4.2).

The area of bare habitat differed by an order of magnitude between sites ($F = 114$, df 1, 238, $P < 0.001$), with a mean of 2.8% ±0.4 (se) at Kettering compared to 20.8% ±1.7 (se) at Hobart. The area covered by other encrusting organisms (including algae) also differed between sites ($F = 315$, df 1, 238, $P < 0.001$), with a mean of 6.7% ±2.1 (se) at Kettering compared to 51.8% ±1.8 (se) at Hobart.

The percent cover of scyphistomae increased with water temperature at Hobart in 2003, with water temperature explaining over 80% of the variation ($F = 43$, df 1,8, $P < 0.001$). However, this relationship broke down in 2004 when water temperature no longer explained the variation ($F = 1.9$, df 1,7, $P = 0.220$, $R^2 = 0.111$), (Table 4.3, Figure 4.3). The percent cover of other encrusting organisms, rainfall, and the area of bare substrate did not explain any of the variation in percent cover of scyphistomae at Hobart in either year.

The percent cover of scyphistomae decreased at Kettering with percent cover of encrusting organisms explaining over 75% of the variation in percent cover of scyphistomae in 2003 and 2004 (2003: $F = 37.6$, df 1,11, $P < 0.001$; 2004: $F = 29.8$, df 1,9, $P = 0.001$). Water temperature, rainfall, and the percent area of bare substrate did not explain any variation in the percent cover of scyphistomae in either year at Kettering (Table 4.3).

Patch Density

There was a three-way interaction (Year*Site*Season) in the patch density of scyphistomae ($F = 12.2$, df 3, 186, $P < 0.001$). Patch density did not change at among seasons Kettering during the two year study,

however there were large differences at Hobart (Figure 4.4). Patch density at Hobart was around two thirds the level of Kettering for the first three seasons of 2003 (summer, autumn, and winter). Patch density increased at Hobart in spring and remained high and at similar levels to that at Kettering through spring, summer, and autumn before falling again to levels approximately two thirds of that at Kettering.

Scyphistomae patch density at Hobart was not related to water temperature, rainfall or the area of bare substrate in 2003. In contrast nearly 95% of the variability was explained by water temperature in 2004 (Figure 4.3) when patch density increased with water temperature ($F = 116$, df 1, 7, $P < 0.001$). Rainfall explained the most variation at Kettering with patch density decreasing as mean daily rainfall increased. Just under 50% of the variation was explained in 2003 ($F = 9.7$, df 1,9, $P < 0.014$), and 50% in 2004 ($F = 10.6$, df 1,11, $P < 0.001$), (Table 4.3, Figures 4.3 & 4.4).

Population Density

There was a Site*Year interaction ($F = 4.2$, df 1, 239, $P = 0.042$), and a Site*Season interaction ($F = 3.4$, df 3, 239, $P = 0.019$), in population density. Population density was higher at Kettering (mean = 313 000 ±13 000 (se) individuals m^{-2}) than at Hobart (mean = 72 800 ±6 300 (se) individuals m^{-2}) in both years ($P < 0.001$ for both years) and in all season ($P < 0.001$ for all seasons). There were no differences at Kettering either between years or among seasons (Figure 4.5). However, there were differences at Hobart where population density was 25% higher in 2004

than in 2003, and where population density in summer was more than double the average in the remaining seasons (Figure 4.5).

Population density at Hobart increased with water temperature, with water temperature explaining nearly 80% of the variation in 2003 ($F = 29.7$, df 1,8, $P = 0.001$), and 60% of the variation in 2004 ($F = 11.5$, df 1,7, $P = 0.03$). However, population density at Hobart was not related to rainfall, the area of other encrusting organisms, or the area of bare substrate. At Kettering, population density of scyphistomae decreased as mean daily rainfall increased with rainfall explaining just under half of the variation in both years (2003: $F = 10.6$, df 1,11, $P = 0.009$; 2004: $F = 6.9$, df 1,9, $P = 0.03$). However, population density at Kettering was not related to water temperature, the area of other encrusting organisms, or the area of bare substrate (Table 4.3, Figures 4.3 & 4.5).

Strobilation occurred at both sites and in both years of the study, however the proportion of scyphistomae strobilating varied between sites and between years. The proportion of scyphistomae that strobilated at Kettering differed between years ($F = 16.1$, df 1,10, $P = 0.005$), with 82% ±14.5 (se) of scyphistomae strobilating in 2003 compared to 30% ±11 (se) in 2004. Strobilation at Hobart occurred at such a low level that it was not detected by the photographic survey in either year, however a thorough visual search on each sampling day did locate some strobilation in each year. Strobilation in 2003 at Kettering occurred over two months from early August to early October. In contrast, in 2004 strobilation was over a shorter six week period from late August to early

October. Strobilation at Hobart was only observed on a single sampling day in 2003 at the end of September and again only on a single sampling day in 2004 at the end of October (Figure 4.3). Strobilation in both years at Kettering began when water temperatures were at ca. 10.5°C and continued into the period when water temperatures began to rise. Strobilation had finished in both years by the time water temperature had reached ca. 12°C (Figure 4.3). Strobilation also occurred among scyphistomae that had colonised the artificial substrates placed at Kettering. These plates had been cleaned three months prior to this sample day, therefore scyphistomae on the plates were less than three months old. The proportion of scyphistomae strobilating on artificial substrates differed to that in the naturally occurring colony ($F = 35.6$, df 1,10, $P < 0.001$), with 19.7% ±9.0 (se) of scyphistomae strobilating on the plates compared to 30% ±11 (se) of scyphistomae in the surrounding colony at the peak of strobilation in 2004. Strobilation did not occur among scyphistomae on the artificial plates at Hobart.

4.3.3 Dynamics of scyphistomae colonising artificial substrates

Percent Cover

The percent cover of scyphistomae on artificial substrates increased through time, however there was a significant Sample Time*Site*Season interaction ($F = 4.0$, df 4,71, $P = 0.006$). Differences at Kettering where due to percent cover at the end of spring being 68% greater than at the end of winter (Figure 4.6). There were no differences among seasons at the Hobart site. The differences of interest between sites were those for each seasons (Figure 4.6). Differences existed between sites in

summer/autumn and in spring with percent cover at kettering 130 times greater than at Hobart by the end of the summer/autumn season ($F = 31.2$, df 2,23, $P < 0.001$), and 10 times greater at Kettering than at Hobart at the end of the spring season ($F = 26.5$, df 2,23, $P < 0.001$). There was no difference between sites in the winter season at the adjusted α level of $\alpha = 0.006$ ($F = 4.1$, df 2,23, $P = 0.04$).

Patch Density

The patch density of scyphistomae on the artificial substrates did not differ between sites ($F = 0.4$, df 2,71, $P = 0.7$), however there were differences among seasons ($F_{Time*Season} = 2.8$, df 4,71, $P = 0.036$), when density in spring was up to 40% greater than in winter across the sampling period ($F = 6.9$, df 2, 47, $P = 0.003$) (Figure 4.7).

Population Density

The population density of scyphistomae increased through time, however there was a significant Sample-Time*Site*Season interaction ($F = 4.1$, df 4, 71, $P = 0.006$). Differences within sites were found at Kettering where population density at the end of winter was half that at the end of spring. There were no differences among seasons at Hobart. The differences of interest among sites were those between like seasons (Figure 4.8). All seasons were different ($F_{summer/autumn} = 38$, df 2,21, $P < 0.001$, $F_{winter} = 18.2$, df 1.2,13.4, $P = 0.001$, $F_{spring} = 61.3$, df 2,21, $P < 0.001$), with population density 11-21 times greater at Kettering than at Hobart by the end of each sample season (Figure 4.8).

Encroachment

The distance scyphistomae had moved onto plates (encroachment) increased through time and the rate of encroachment was dependant on site ($F_{Time*Site} = 30$, df 2,71, $P < 0.001$), with encroachment three times greater at Kettering than at Hobart (Figure 4.9 (a)). This equated to a mean rate of encroachment during each experimental season of 1.5mm day^{-1} at Kettering and 0.5mm day^{-1} at Hobart. The rate of encroachment also depended on season ($F_{Time*Season} = 3.1$, df 4,71, $P = 0.021$), where encroachment in spring was 40% greater than in winter (Figure 4.9 (b)).

4.4 Discussion

This study showed that a combination of biotic and abiotic factors were involved in determining the potential for a bloom of *Aurelia* sp. medusae, in the form of number of ephyrae liberated, in any given year in south east Tasmania. The number of ephyrae liberated is directly related to the size of the benthic scyphistomae population at the time of strobilation (Brewer and Feingold 1991, Watanabe and Ishii 2001, Colin and Kremer 2002), the proportion of those scyphistomae strobilating, and the number of ephyrae produced per individual scyphistomae. The size of colonies of *Aurelia* sp. scyphistomae, and therefore their population size, was ultimately physically restricted by the total available area of their preferred habitat (flat undersurfaces of hard substrates). Superimposed on this were spatial and temporal variations in the density of scyphistomae and the degree of strobilation within colonies. Factors including temperature, salinity, competition for space, and geographic

location were linked with the observed differences between colonies and among seasons in south east Tasmania.

4.4.1 Colony Dynamics

With the availability of suitable habitat being a limiting factor for the size of benthic scyphistomae populations, maximizing the number of scyphistomae present on the available habitat at the time of strobilation is critical to the success of Aurelia sp. in south east Tasmania. Key indicators of colony performance in this study were the density of scyphistomae at each site (population density), the proportion of the population strobilating and the duration of strobilation. The performance of scyphistomae colonies varied both between sites and among seasons. Population densities were consistently higher at Kettering than at Hobart with densities up to 14 times higher on natural substrates and up to 21 times higher on artificial substrates. Higher population densities on natural substrates at Kettering were primarily due to patches of scyphistomae occupying a greater proportion of the substrate. However, a lower density of scyphistomae within patches at Hobart during parts of the study further contributed to the observed differences in population density. Strobilation was also far greater at Kettering, occurring over a 6-8 week period in spring and with up to 80% of the scyphistomae strobilating at that site compared to levels so low at Hobart that they were not detected by the survey. The differences in the colony dynamics between the sites showed the conditions at Kettering during the study period were more favorable for scyphistomae growth and reproduction than the conditions at Hobart.

The inverse linear relationship between the area covered by scyphistomae and the area covered by other encrusting organisms at Kettering suggests that competition for space was limiting colony growth. Increased mortality of *A. aurita* scyphistomae has been attributed to competition for space from other encrusting organisms (Watanabe and Ishii 2001). Interspecific competition for space has also been found to be a major controlling factor of density in *Cyanea* sp. scyphistomae (Colin and Kremer 2002) while rates of colony growth and therefore density of *A. aurita* scyphistomae can change according to environmental conditions and density dependant effects (Coyne 1973, Watanabe and Ishii 2001, Fischer and Hofmann 2004). Mortality rates can also change according to environmental conditions experienced by the scyphistomae as well as through changes in predation pressure (Gröndahl and Hernroth 1987, Keen 1991). There was no relationship between the area covered with scyphistomae and the area covered with other encrusting organisms at Hobart, and over 20% of the substrate was bare. This indicated that competition for space was not the limiting factor for scyphistomae population size at that site, and that other factors were acting to affect the ability of *Aurelia* sp. scyphistomae to maximize their use of the available habitat.

Water temperature and rainfall (as a proxy for salinity) both explained significant amounts of the variation seen in the population density of scyphistomae in south east Tasmania. The finding of a positive correlation with temperature agrees with other studies that show rates of asexual reproduction in *A. aurita* in experimental situations increase

with water temperature (Keen 1991, Omori *et al.* 1995, Miyake *et al.* 2002). The relationship with salinity however is much more poorly understood with some reports suggesting salinity has little direct effect on scyphistomae reproduction in *A. aurita* (Halisch 1933, Watanabe and Ishii 2001), but may effect mortality of *A. aurita* (Watanabe and Ishii 2001) and asexual budding of *Chrysaora quinquecirrha* (Purcell *et al.* 1999b). These results indicate that salinity may have been having an effect on reproduction in *Aurelia* sp. although the exact nature of this relationship is uncertain. For example rainfall may be correlated with other variables such as food availability, which has also been positively correlated with rates of budding in scyphistomae (e.g. Hernroth and Gröndahl 1985b, Lucas 2001).

Annual and seasonal differences in the percent cover, patch density, and population density of scyphistomae were not observed in the naturally occurring colony at Kettering where space was limiting, however, differences in these variables at these scales were observed in the naturally occurring colony at Hobart where space was not limiting. A change in population density will occur when the rate of mortality differs to the rate of bud production and recruitment of daughter polyps to the substrate (Lucas 2001). Space was removed as a limiting factor by deploying artificial substrates. Other density dependent effects, including food availability and water quality, may also have been reduced (Harper 1985). Under these circumstances a seasonal environmental effect on the dynamic relationship between budding and mortality became apparent. This shows that factors contributing to seasonal

differences in colony growth were present at both sites and that the rates at which new or recovering colonies will be able to expand to their maximum densities will be governed by these same factors. No additional information about annual patterns was gained from the artificial substrates as this portion of the study only covered a single year. Factors contributing to seasonal differences in colony size and growth were assumed to be those environmental variables detected by regression analysis (e.g. Keen 1991, Omori *et al.* 1995, Watanabe and Ishii 2001, Miyake *et al.* 2002), however these factors were not as important for determining colony size as competition for space where space was limiting (e.g. Harper 1985).

No evidence of predation contributing to the differences in scyphistomae population size was observed during this study. Elsewhere predator populations numerically increase in response to large populations of scyphistomae, with the resulting increase in predation pressure leading to a rapid reduction in the numbers of scyphistomae in colonies (Gröndahl and Hernroth 1987, Keen 1991). It has been suggested that scyphistomae density is primarily determined by the number of larvae settling and metamorphosing onto the substrate (Watanabe and Ishii 2001). However, recruitment of planula larvae to the substrate is unlikely to have contributed to the observed differences between sites because medusae were not only scarce or absent in the summers during the study, but the main periods of increase in density of scyphistomae in colonies occurred through spring prior to medusae being present. The absence of medusae in the Derwent Estuary during the

study, along with the observed presence of the colony a year prior to, and it's persistence a year following this study (pers. obs.) showed that the colony has survived asexually for at least four years. This agrees with observations of *A. aurita* scyphistomae in the laboratory where colonies persisted for four years (Gong 2001). Given the nature of asexual reproduction it is likely that a population could survive indefinitely as an entity, with a continual turnover of new individuals replacing those dying (Jackson 1985), however this may eventually limit genetic diversity in the colony (Keen and Gong 1989, Keen 1991, Gong 2001).

Continued population growth was observed on artificial substrates alongside stable populations on the natural substrates at Kettering. If density dependant controls were operating they must have been at the individual scyphistomae level, otherwise growth would not have been observed on the bare artificial substrates. It was not determined whether limited space at Kettering caused a reduction in the number of buds produced or if young scyphistomae suffered higher mortality through intra-specific predation. High mortality of newly released buds of the scyphozoan *Cotylorhiza tuberculate* occurs when density of established scyphistomae is high (Kikinger 1992), however *A. aurita* scyphistomae were not aggressive to conspecifics (Keen 1991). Alternately, newly detached buds may simply have failed to successfully recruit to the substrate and have fallen from the colony surface.

The pattern of increase in population density on artificial substrates provided an indication of how quickly new colonies of scyphistomae may be able to colonise any available habitat. The highest rates of increase in

population density were seen in spring, which corresponds to the period immediately following strobilation. Scyphistomae are likely to be small with depleted body reserves immediately following strobilation and colonies may have experienced higher than normal mortality at this time (Watanabe and Ishii 2001). The high growth rates of colonies seen in spring are an indication that conditions during this period are likely to be ideal for colonies to rebuild following strobilation. Although no *in situ* estimates of the seasonal pattern of zooplankton abundance were available during this study, previously published zooplankton data from south east Tasmania suggests that a spring bloom of phytoplankton occurs each year (Harris *et al.* 1991, Cheshuck 2001). In addition, with strobilation having just occurred, newly released ephyrae will have access to the same productive bloom conditions benefiting the scyphistomae.

4.4.2 Strobilation

Population size at the time of strobilation is clearly important for maximizing the success of the life cycle of scyphozoans. Of equal importance must also be the proportion of the population which strobilates, and the number of ephyrae produced per scyphistoma. Strobilation was observed in both years and at both colony locations at the end of the cool winter period. However, there were significant differences in the proportion of scyphistomae involved, and the duration of the strobilation period, with more scyphistomae strobilating, and strobilation continuing over a longer period at Kettering than at Hobart. Differences in the amount of strobilation at each site again highlight the

difference in the suitability of each location for supporting a healthy scyphistomae population.

Strobilation in *Aurelia* sp. scyphistomae occurred as water temperatures began to rise following winter. These findings agree with studies of *A. aurita* that found strobilation occurs following minimum winter water temperatures (Palmen 1953, Custance 1964, Rasmussen 1973). Although strobilation was occurring as water temperatures were rising in spring, it had begun prior to any warming taking place. This suggested that spring warming of the water column was not the cue for strobilation to commence, however, water temperature may have some control over the timing of strobilation and the proportion of the population strobilating. Strobilation started later, ended sooner, and fewer scyphistomae strobilated in 2004 when winter water temperatures were one degree cooler than the previous year. These results are consistent with those of *A. aurita* which saw delays to strobilation in cooler years (Purcell *et al.* 1999b, Lucas 2001). Strobilation at Kettering started when water temperature was the same in both years, and finished when water temperatures were the same in both years. This indicates that strobilation may have been tightly constrained by water temperature, however, observations over more years are necessary. This type of tight control of the onset and conclusion of strobilation in *Aurelia* spp. by temperature has not been reported before.

Strobilation in south east Tasmania began around 1.5 months after the coldest water temperatures were reached in both years, but had commenced before a spring bloom would be expected (Harris *et al.* 1991,

Cheshuck 2001). No information was available on differences in food availability between sites, however the onset of strobilation in scyphozoans has been reported to occur when zooplankton biomass is high (Henroth and Gröndahl 1985a, Keen 1991). Further, higher food availability leads to higher ephyrae production (Papathanassiou *et al.* 1987, Olesen *et al.* 1994, Lucas 1996, Ishii and Båmstedt 1998). The release of ephyrae and growth of juvenile medusae would be more likely to coincide with such a spring bloom in south east Tasmania which may have important ramifications for successful recruitment to the adult population. Additionally, the low levels of strobilation observed at Hobart may have been due in part to lower food availability at this site.

The observed spatial variability in strobilation suggests that scyphistomae are able to reduce or postpone strobilation in years when conditions are not favourable for ephyrae production or ephyrae survival. This is contrary to reproductive theory that suggests production of dispersive rametes (ephyrae) will occur when conditions are least favourable in an effort to ensure survival of the genotype (Roff 1992). Alternately, an inverse relationship between density and the timing of onset of strobilation (Silverstone *et al.* 1977, Keen 1991) may explain the delay in the strobilation that was observed at Hobart relative to the timing of strobilation at Kettering. If onset of strobilation is density dependant then there is the possibility that density at Hobart was below the threshold necessary for strobilation to occur at this site. Poor nutrition can also affect the number of ephyrae produced (Spangenberg 1968), but there are no reports of whole colonies failing to reproduce,

although some clone types can fail to strobilate in the laboratory (Gong 2001). Asexual reproduction in scyphistomae is dependant on the environmental conditions in which they find themselves and it is possible that a dynamic balance between environmental variables, in particular food, temperature, and salinity, specific to individual populations is governing timing and magnitude of the scyphistomae response (Lucas 2001).

This study showed that there were clear spatial and temporal differences in the population dynamics of colonies of scyphistomae. Density dependent effects controlled budding and recruitment of new scyphistomae to the substrate when population density was high and space was limiting, while environmental controls of budding and strobilation were operating when space was not limiting. Water temperature and rainfall were linked to changes in population size, however the mechanisms by which the balance between reproduction and mortality was affected clearly require clarification.

Table 4.1 Summary of studies examining environmental factors involved in regulating population size and rates of asexual reproduction in the scyphistomae.

Mode of asexual reproduction	Factor	Author(s)
Population size	predation	Hernroth and Gröndahl (1985a, b)
	density	Coyne (1973), Gröndahl (1988a)
	interspecific competition	Gröndahl (1988a)
	habitat availability	Miyake *et al.* (2002)
Vegetative budding	food availability	Coyne (1973), Gröndahl (1988a), Keen and Gong (1989)
	water temperature	Coyne (1973), Kakinuma (1975)
	orientation of the substrate	Brewer (1978), Gröndahl and Hernroth (1987), Watanabe and Ishii (2001)
Strobilation	changes in temperature	Rasmussen (1973), Brewer and Feingold (1991), Purcell *et al.* (1999b)
	illumination	Custance (1964), Kakinuma (1975)
	salinity	Brewer and Feingold (1991)
	food availability	Keen (1991), Watanabe and Ishii (2001)

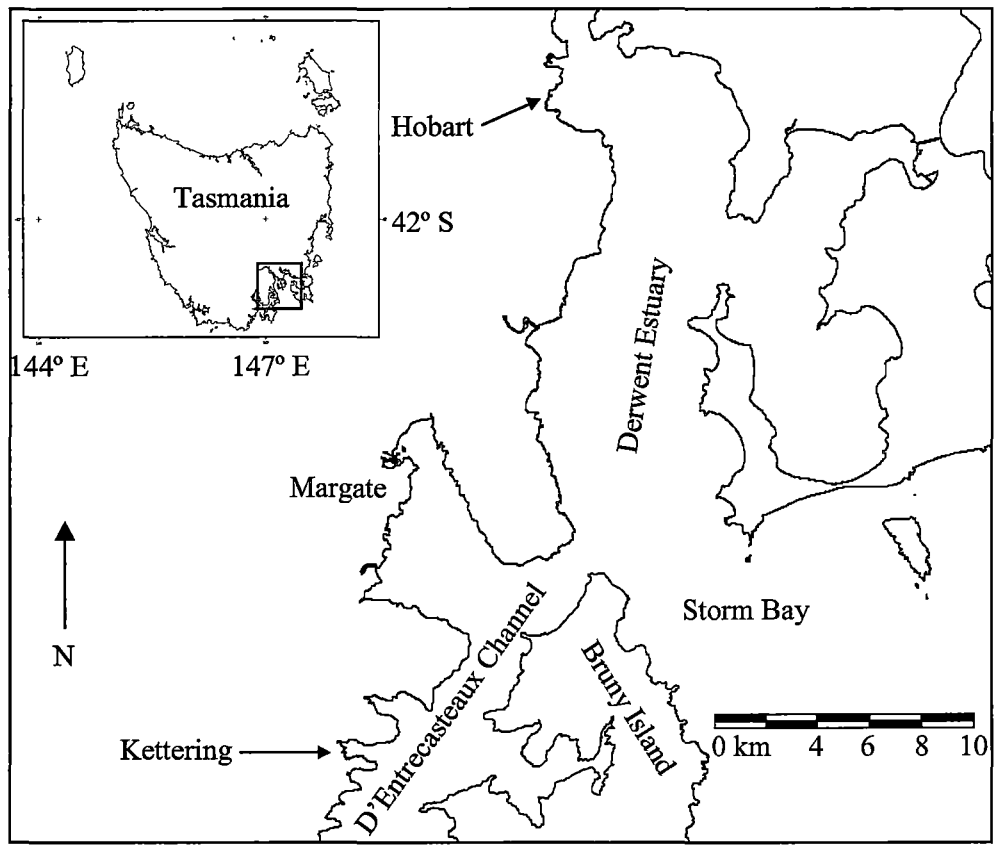

Figure 4.1 Location of the scyphistomae colony study sites at Hobart and Kettering in south east Tasmania.

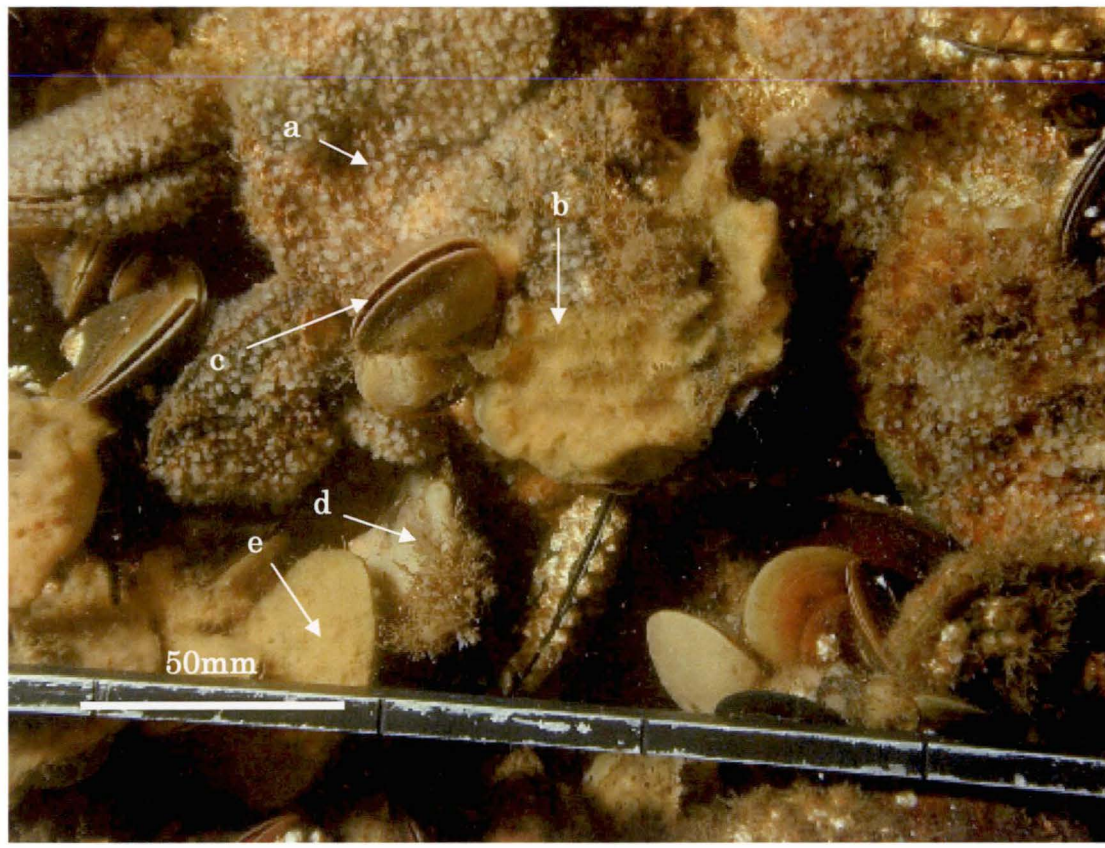

Plate 4.1 An example of a photograph of the *Aurelia* sp. scyphistomae colony located at Hobart with; (a) scyphistoma, (b), encrusting sponge, (c) bare mussel, (d) algae, and (e) scale bar on camera framer.

Table 4.2 Description of the categories assigned to benthic photograph subject matter for use in quantifying differences among colony sites and among sampling periods.

Category	Description
Scyphistomae (non-strobilating)	⇒ any substrate covered by scyphistomae which were not clearly in the process of strobilating
Scyphistomae (strobilating)	⇒ any substrate covered by scyphistomae which were clearly in the process of strobilating
Bare	⇒ any bare substrate potentially available for scyphistomae for attachment and includes exposed concrete or acrylic plate, bare oyster and mussel shells, and ascidians
Algae	⇒ any part of any algal species attached to and covering any substrate
Other	⇒ any biofouling organisms which were not used by scyphistomae as habitat and includes sponges and bryozoans
Obscure	⇒ any area of substrate not clearly visible in an image and includes fish, starfish, shadows, and areas covered by the camera framer

Table 4.3 Relationships between environmental variables (water temperature, mean daily rainfall, % cover of other encrusting organisms) and scyphistomae colony variables.

Kettering							
Dependent Variable (a)	**Year**	**Independent Variable (x)**	**Intercept (c)**	**Slope (b)**	**Variability Explained (r2)**	**P**	**se**
Percent cover of scyphistomae (%)	2003	% cover encrusting	98.4	-1.21	79% (0.79)	<0.001	1.95%
	2004	% cover encrusting	96.6	-0.9	79% (0.79)	0.001	1.8%
Patch density (thousands m-2)	2003	Mean daily rainfall	402.0	-19.3	49% (0.49)	0.012	35 741
	2004	Mean daily rainfall	418.4	-33.8	55% (0.55)	0.014	34 902
Population density (thousands m-2)	2003	Mean daily rainfall	356.5	-17.7	52% (0.52)	0.009	31 103
	2004	Mean daily rainfall	390.5	-33.3	46% (0.46)	0.030	40 809
Hobart							
Dependent Variable (a)	**Year**	**Independent Variable (x)**	**Intercept (c)**	**Slope (b)**	**Variability Explained (r2)**	**P**	**se**
Percent cover of scyphistomae (%)	2003	Mean water temperature	-63.7	6.7	86% (0.86)	<0.001	7.98%
	2004	Mean water temperature	8.5	1.5	24% (0.24)	0.22	8.3%
Patch density (thousands m-2)	2003	Mean water temperature	32.7	-4.6	4% (0.04)	0.6	65820
	2004	Mean water temperature	-8.8	21.9	95% (0.95)	<0.001	15850
Population density (thousands m-2)	2003	Mean water temperature	-14.6	15.9	81% (o.81)	0.001	22783
	2004	Mean water temperature	-56.7	11.1	66% (0.66)	0.015	25533

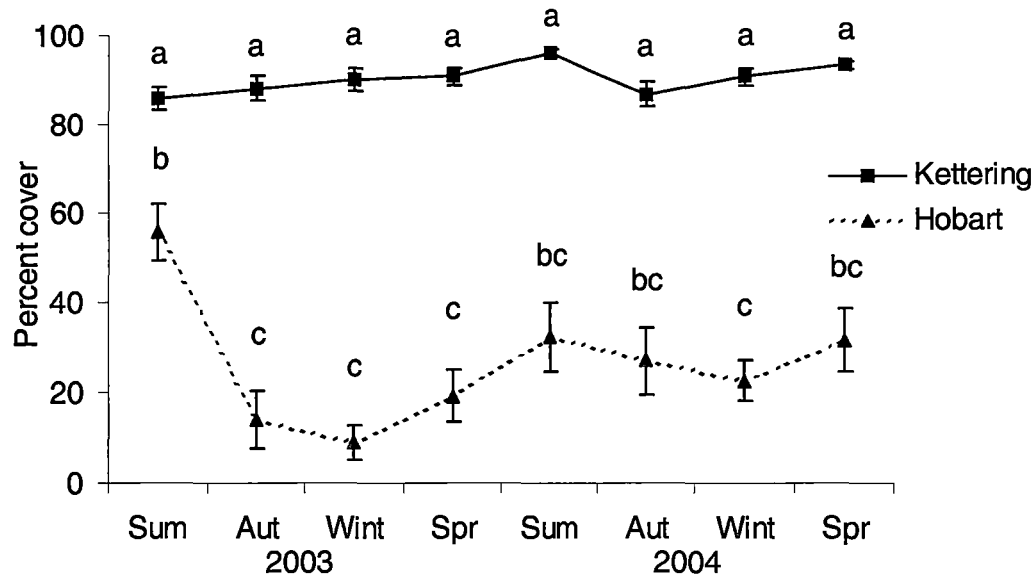

Figure 4.2 The percent cover (±se) of the natural substrate covered by scyphistomae (n = 12 for Kettering, n = 18 for Hobart). Means with different letters were significantly different as determined by Tukey's HSD tests.

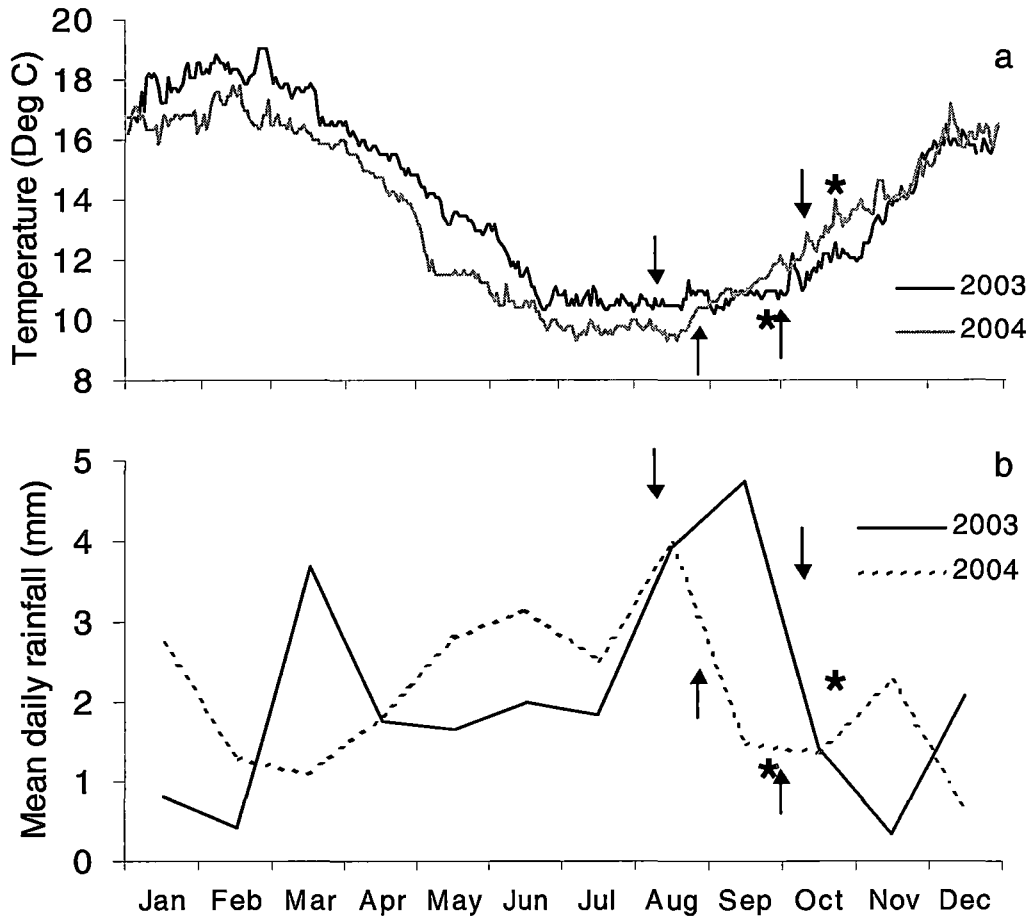

Figure 4.3 a) Daily water temperature measured at Kettering and b) mean daily rainfall measured at Margate. Arrows above the line (pointing down) indicate the timing of the first and last observation of strobilation at Kettering in 2003 and arrows below the line (pointing up) indicate the timing at Kettering in 2004. Strobilation at Hobart was only noted on one sample day each year and is indicated by stars (above the line, 2003, below the line, 2004).

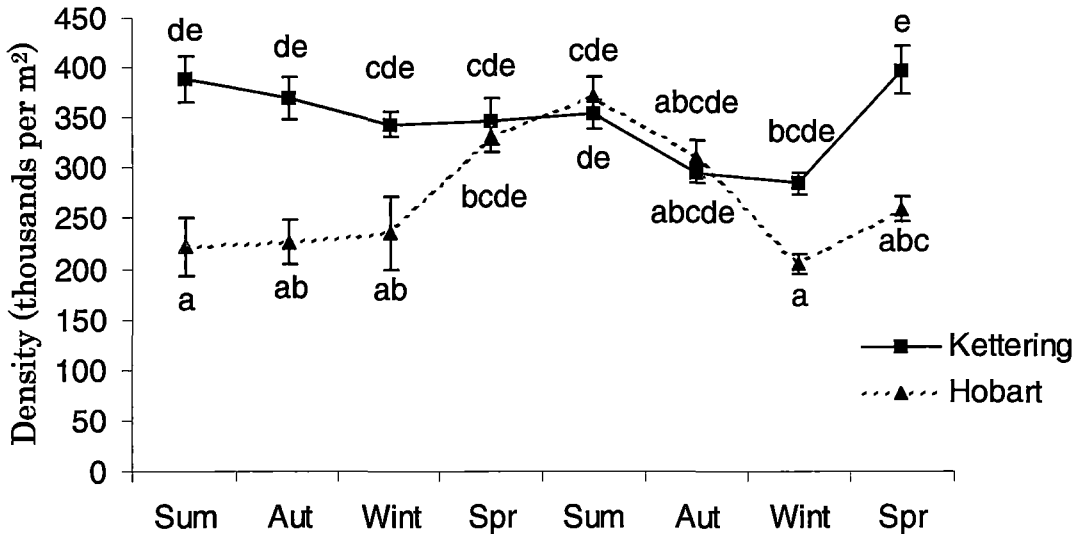

Figure 4.4 Mean density (±se) of scyphistomae within patches (n = 12 for Kettering, n = 18 for Hobart). Means with different letters were significantly different as determined by Tukey's HSD tests.

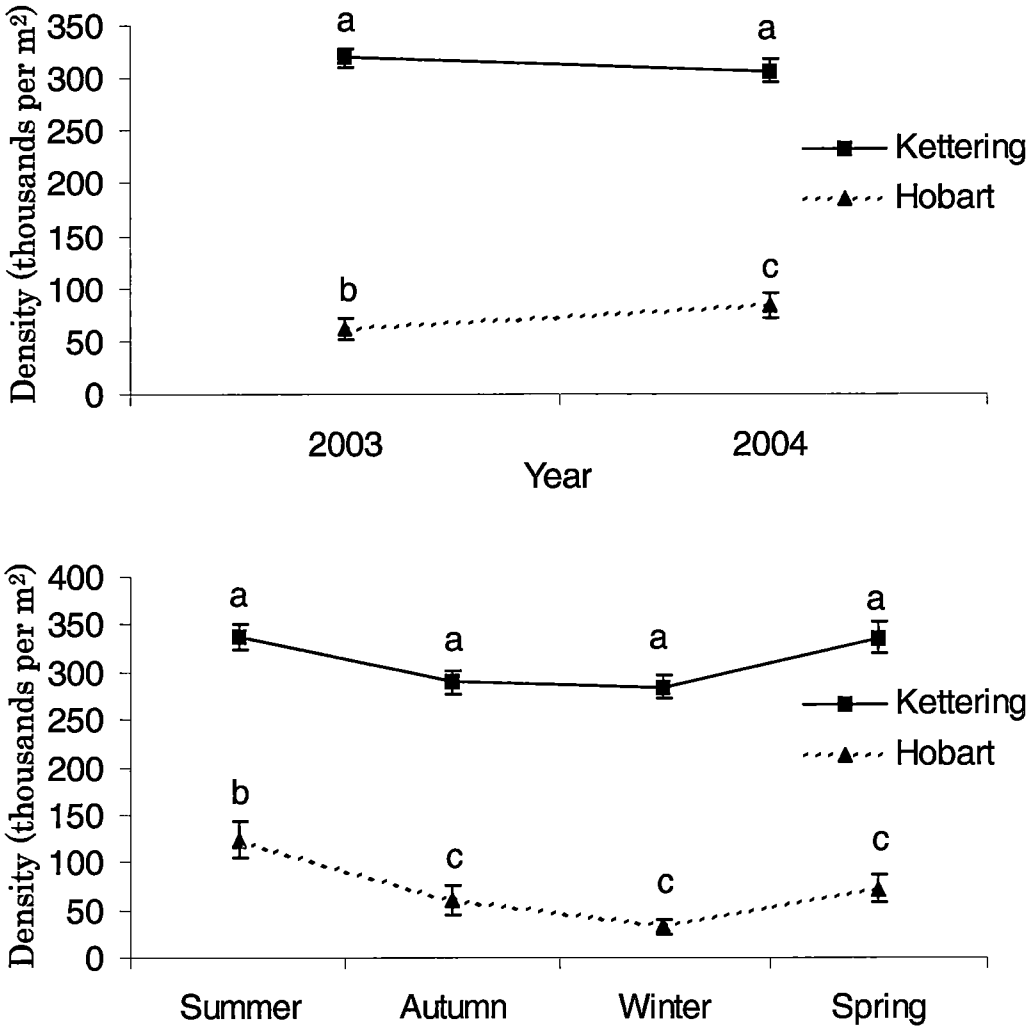

Figure 4.5 Mean population density (±se) of scyphistomae for: (a) the Year*Site interaction (n = 48 for Kettering and n = 72 for Hobart), and (b) the Season*Site interaction (n = 24 for Kettering and n = 36 for Hobart). Means with different letters were significantly different as determined by Tukey's HSD tests.

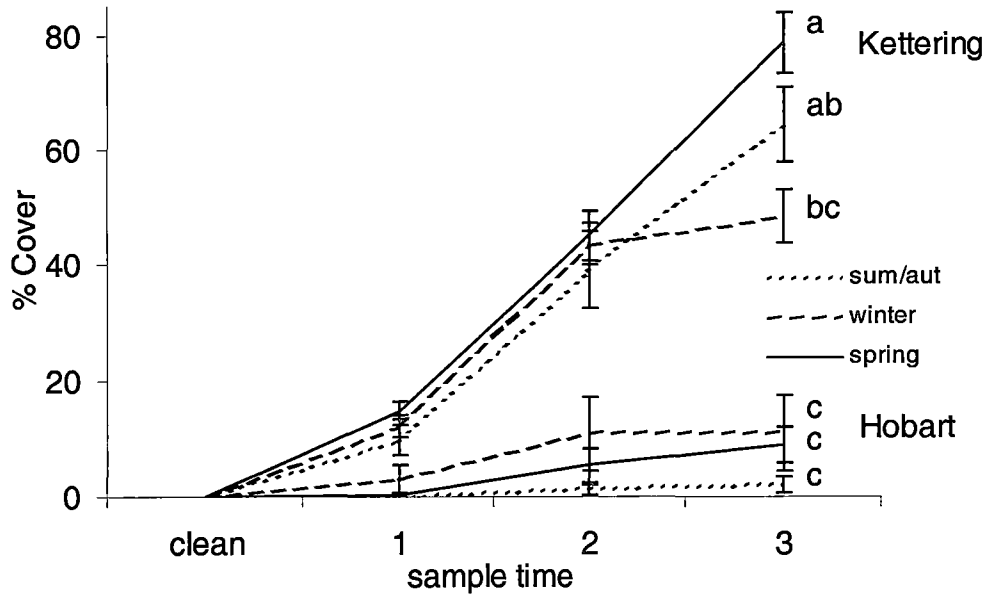

Figure 4.6 The pattern of increase in the percent cover (±se) of scyphistomae on artificial substrates following plate cleaning in three different seasons at Kettering and at Hobart (n = 6). Letters indicate where seasonal patterns were different between sites and among seasons as determined by repeated measures ANOVA.

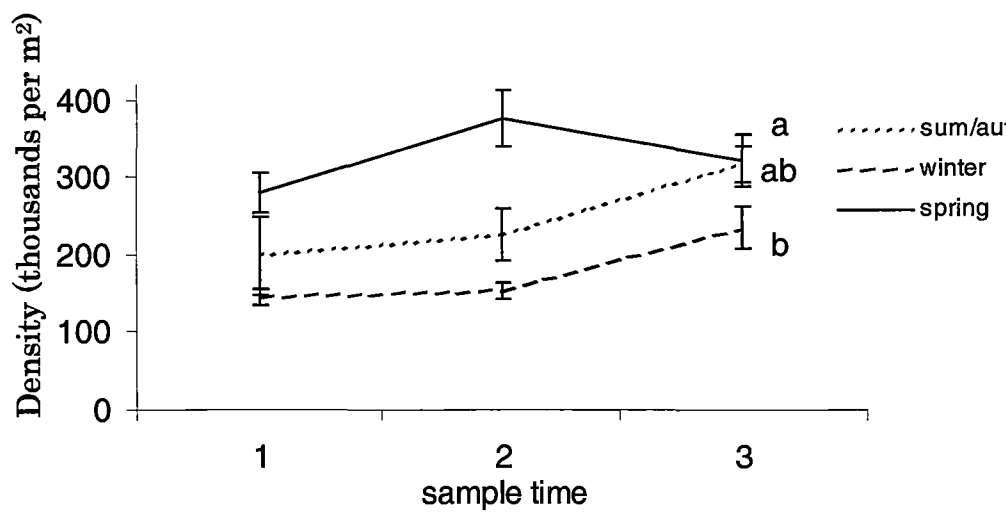

Figure 4.7 The pattern of density of scyphistomae within patches (±se) on artificial substrates following plate cleaning in three seasons (n = 12). Letters indicate where seasonal patterns were different as determined by repeated measures ANOVA. Site data has been pooled for graphing.

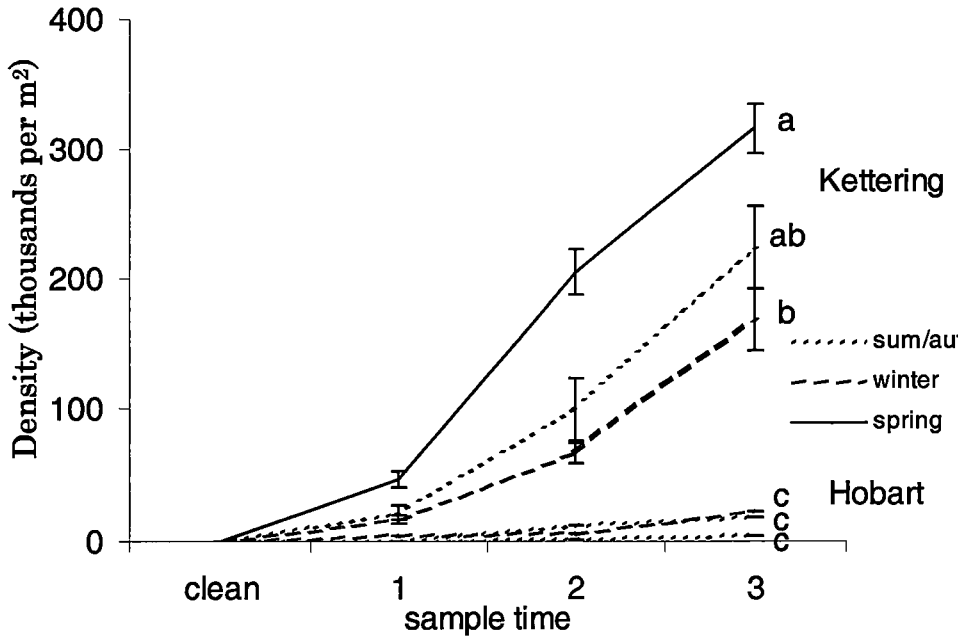

Figure 4.8 The pattern of increase in population density (±se) of scyphistomae on artificial substrates following plate cleaning in three different seasons at Kettering and Hobart(n = 6). Letters indicate where seasonal patterns were different between sites and among seasons as determined by repeated measures ANOVA.

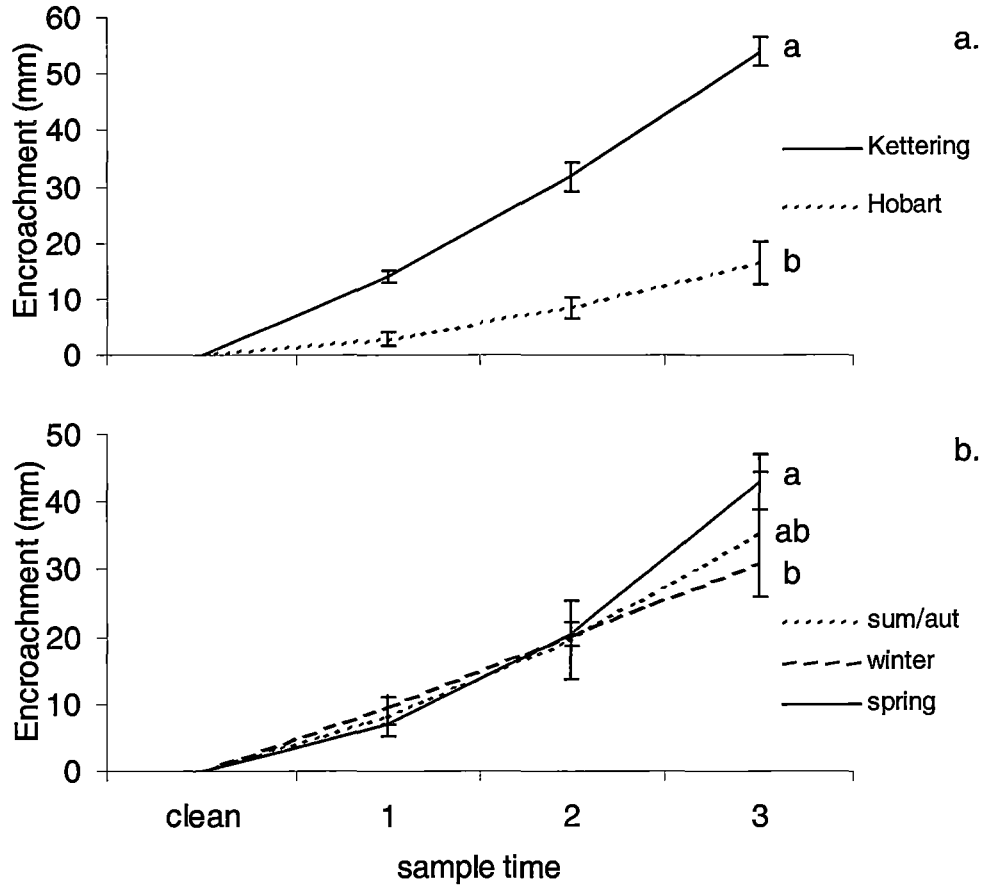

Figure 4.9 The distance (±se) scyphistomae had moved onto artificial substrates (encroachment) following plate cleaning for: a.) the Time*Site interaction(n = 18), and b.) the Time*Season interaction (n = 12). Letters indicate where seasonal patterns were different as determined by repeated measures ANOVA.

CHAPTER 5:

EFFECTS OF TEMPERATURE AND SALINITY ON ASEXUAL REPRODUCTION IN SCYPHISTOMAE OF *AURELIA* SP.: AN EXPERIMENTAL STUDY

5.1 INTRODUCTION

Outbreaks of jellyfish blooms are an increasingly common phenomenon around the world (Lucas 2001). Juvenile pelagic stages (ephyrae) of many jellyfish species develop from asexual benthic scyphistomae, therefore the abundance and behaviour of scyphistomae can have a direct impact on the success of recruitment of the ephyrae to the mature medusae population (Brewer and Feingold 1991, Gong 2001, Colin and Kremer 2002). Reproduction in scyphistomae is asexual and occurs either by vegetative budding or by strobilation producing ephyrae (e.g. Spangenberg 1964a).

The reproductive response of scyphistomae represents a trade-off between the two modes of asexual reproduction with scyphistomae making a choice between more ephyrae, or more scyphistomae in the colony. Increased investment in the quality and quantity of ephyrae increases the likelihood of successful recruitment to the important sexual medusae phase, while increased investment in budding increases the likelihood of survival of the population and provides a larger base from which to produce the dispersive rametes in the future (Brewer and Feingold 1991, Stearns 1992, Purcell *et al.* 1999b).

The allocation of energy resources to each mode of asexual reproduction can vary according to environmental conditions experienced by the scyphistomae (e.g. Keen and Gong 1989, Purcell *et al.* 1999b, Gong 2001). Numerous factors capable of modifying the rate and timing of asexual reproduction in scyphistomae have been identified (Table 5.1). Current understanding of the interplay between environmental

conditions and colony dynamics of *Aurelia* spp is predominantly restricted to responses at the whole colony level; that is, how does colony size change and how many ephyrae are produced (e.g. Spangenberg 1964a, Purcell *et al.* 1999b, Watanabe and Ishii 2001). However, processes leading to these responses remain poorly understood (Lucas 2001) and yet are amongst the most important for understanding colony dynamics (Garrabou 1999). The only studies at the level of individual scyphistoma have focused on the range of responses of selected clone types (Gong 2001).

This study aims to determine the responses of *Aurelia* sp. scyphistomae, at the level of the individual, and at the level of the whole colony, to temperature and salinity regimes likely to be encountered in their natural environment in south east Tasmania (CSIRO 2000). The effect of temperature on *A. aurita* scyphistomae has been previously reported (Coyne 1973, Kakinuma 1975, Keen 1991), however the effect of salinity, and its interplay with temperature, is much more poorly studied. Responses such as what proportion of the scyphistomae population are asexually active, how many buds are developing on scyphistoma, and how scyphistomae change size were examined at the level of the individual, while population growth, mortality, and response times were examined at the level of the whole colony. This multi-level approach has provided a more complete picture of the reproductive strategy of *Aurelia* sp. Additionally, breaking the life cycle down and studying some of the components in detail has provided insight into how these obvious environmental variables may be acting on individual parts of the life

cycle and how this in turn may affect recruitment success to the highly aggregative adult medusae stage.

5.2 METHODS

Aurelia sp. polyps were collected in January 2004 from a naturally occurring polyp colony located on the under-side of a floating marina at Kettering in the D'Entrecasteaux Channel in south east Tasmania. Dead oyster and mussel shells with large numbers of polyps attached were randomly removed from the underside of the marina and transported to the Marine Research Laboratories at Taroona in 20L drums filled with seawater from the colony site. Polyps were gently removed from the shells and transferred to the surface of flat black acrylic plates using a flexible metal blade and a wide mouth pipette. The acrylic plates (60mm x 100mm x 3mm) were prepared beforehand by lightly abrading their surface with steel wool followed by a thorough wash before being covered with filtered seawater and left to condition. The plates were laid flat in a large plastic tray and covered with approximately five centimetres of filtered seawater and approximately 30 polyps were placed on the centre of each plate. They were then left undisturbed in the dark for five days allowing polyps time to attach to the plates. Each plate was examined using a stereo microscope and damaged, deformed or poorly attached polyps were removed. This left a replicate experimental "colony" containing a known number of individuals (9-19 polyps) on each plate representing a random sub-sample of the naturally occurring population. The response of the replicate colonies to experimental treatment regimes

was assumed to represent the response of the natural population as closely as possible.

To determine the effect of temperature and salinity on polyp colony population dynamics, a two factor orthogonal design was used with three temperatures (10°C, 13°C, and 16°C) and three salinity treatments (25‰, 30‰, and 35‰) over a 32 day period. Temperature and salinity levels were chosen to represent the range of conditions which naturally occurring polyps are likely to be exposed to in a typical seasonal cycle in south east Tasmanian estuaries (CSIRO 2000).

The experimental apparatus consisted of three temperature controlled water baths set to each level of temperature treatment. Each water bath contained three salinity treatment levels with three replicates colonies. Replicate colony plates were individually suspended vertically in one litre glass jars with gentle aeration. Care was taken to avoid bubbles contacting the surfaces of the plate with polyps attached. Polyps were fed *Artemia* sp. (nauplii to 24 hour old) daily at a level which ensured that food was constantly present in all treatments. Plates were transferred to new one litre jars of filtered seawater, pre-conditioned to the correct temperature and salinity, every second day to maintain water quality. Water temperature was maintained (± 0.2°C) at the set treatment level within water baths. Salinity in each replicate jar was measured daily and lowered using distilled water or raised using Fossey Sea Salt where necessary.

Every 2-4 days each plate was examined using a stereo microscope. This was done by placing the plates horizontally in a shallow dish

containing filtered seawater pre-conditioned to the replicate temperature and salinity treatment level. The number of polyps present in each colony on each sample day, the number of buds present in colonies, and the number of polyps actively producing buds within colonies were recorded (Plate 5.1). An individual bud was defined as a developing polyp which was still attached to the parent polyp, while an actively budding polyp was any polyp which had one or more developing buds attached. The diameter of a random sub-sample of polyps was measured on the last day of the experiment (Day 32) to determine if individual size was affected by experimental conditions. Any polyp that had died or had become detached and fallen from the plates was counted and removed. Any sign of the onset of strobilation among treatments was also looked for on each sample day.

In an effort to induce strobilation following the 32 day experimental period potassium iodide was added to each treatment at the concentration shown by Silverstone *et al.* (1977) to be the most effective at initiating strobilation (10^{-4}M) while maintaining the polyps within their temperature and salinity treatments.

5.2.1 Statistical analysis

Population growth:

A split-plot design repeated measures ANOVA was used to examine the effect of temperature and salinity on the growth rate of colonies, using a log10 transformation due to heterogeneity of variances. Where the repeated measures ANOVA assumption of sphericity was violated, degrees of freedom for the univariate F-tests were adjusted downwards

based on the Greenhouse-Geisser estimate of epsilon (ε) (Quinn and Keough, 2002).

Where significant effects involving time were found using the repeated measures ANOVA, a one-way ANOVA at each sample day was used to identify the point in time at which colony size became significantly different between treatment levels. Tukey's HSD *t*-tests were used to determine which pairs of treatment means were significantly different. Paired Sample *t*-Tests were used to identify the point in time at which colony size had changed significantly from the start of the experiment for each treatment level. Each pair of means tested consisted of the mean number of polyps in a treatment on Day 1 and the mean number of polyps in a treatment on each successive sample day. Critical probability values were adjusted for multiple tests using the Bonferroni correction (Quinn and Keough, 2002) to $\alpha = 0.007$ for comparisons among the three treatment groups and to $\alpha = 0.004$ when comparing among the 13 sample dates.

Number of buds:

Repeated measures ANOVA of the number of developing buds present in colonies could not be conducted because of the dependence of this measure on a covariate, the number of polyps in the colony. Instead, an ANCOVA among treatments was conducted for each sample day.

Number of actively budding scyphistomae:

Analysis of covariance (ANCOVA) was used to examine the effect of temperature and salinity on the last day (Day 32) of the experiment on the proportion of polyps in colonies that were actually producing buds,

where the number of polyps in a colony was used as the covariate. Similarly the number of buds present on actively budding polyps was analysed using the number of buds present (log10 transformed) with the number of actively budding polyps used as the covariate. The proportional number of buds present in whole colonies was analysed using the number of buds present as the response (log10 transformed) with the number of buds in each colony as the covariate. Adjusted means were compared using the modified *t*-test (Quinn and Keough, 2002) when significant differences were identified between treatments.

Scyphistomae size:

Polyp diameter data were grouped into four size classes: <1.9mm, 2–2.9mm, 3–3.9mm and 4–4.9mm. Chi square tests of independence were used to compare frequency distributions between treatments. Standardised residuals (ie differences between expected and observed frequencies) were used to determine where the departure of independence between the two variables of size class and treatment occurred.

Mortality:

ANCOVA was used to examine the effect of temperature and salinity on polyp mortality on each sample day. The number of polyps in colonies was log10 transformed due to heterogeneity of variances and used as the covariate.

Interaction terms were tested for all analyses and where significant, this term was explored using the tests outlined above and presented graphically. Where the interaction term was not significant the main

effects were explored using the tests outlined above and presented graphically.

5.3 RESULTS

5.3.1 Population growth

The number of polyps increased through time, but the rate of increase depended upon temperature ($F = 15.1$, df 5.6, 51.1, $P < 0.001$) (Figure 5.1) while salinity had no effect ($F = 0.81$, df 5.7, 51.1, $P = 0.561$). Increases in treatment means were not significant up until around Day 19. By Day 21 the number of polyps in both the 13°C and 16°C treatments had increased by 20% and 36% respectively from the number at the start of the experiment ($\alpha = 0.004$, 13°C; $t = -6.5$, df 8, $P < 0.001$, 16°C; $t = -6.0$, df 8, $P < 0.001$) (Figure 5.1). No significant increase in the number of polyps occurred in the 10°C treatment throughout the experimental period. At the end of the experimental period (Day32) the mean increase in population size was 8%, 93% and 189% in the 10°C, 13°C and 16°C treatments respectively (Figure 5.1). Around Day 19 there was a separation between temperature treatment means with the colony increasing in size at a faster rate at higher temperatures. The difference between temperature treatments was significant on the last two sample days (Days 29 and 32) ($\alpha = 0.004$, Day 29; $F = 8.35$, df 2,24, $P = 0.002$, Day 32; $F = 9.95$, df 2,24, $P = 0.001$). The difference was between the highest and the lowest temperature treatments ($\alpha = 0.004$, Day 29; $P < 0.001$, Day 32; $P < 0.001$) (Figure 5.1) where the average population size in the 16°C

treatment was approximately double the size of that in the 10°C treatment.

5.3.2 Number of buds

The number of buds present on polyps differed significantly among the three temperatures but not among the three salinity levels. Differences were detected on Days 14, 17, and 21 ($\alpha = 0.004$, Day 14; $F = 8.3$, df 2, $P = 0.002$, Day 17; $F = 12.6$, df 2, $P < 0.001$, Day 21; $F = 12.5$, df 2, $P < 0.001$) (Figure 5.2). On Day 14 and Day 17 there were approximately twice the number of buds present in the 16°C treatment than in the 10°C and 13°C treatments, which had a similar amount to each other. All treatments were significantly different on Day 14, however by Day 17 the 10°C and 13°C treatments were not different (Figure 5.2). On Day 21 the number of buds in the 16°C treatment was approximately 1.5 times higher than that in the 13°C treatment which was in turn approximately twice as high as in the 10°C treatment. The difference between temperatures was not significant on the remaining four sample days (Days 24, 26, 29 and 32), however the 10°C treatment averages remained at approximately half that of both the 13°C and 16°C treatments.

The slope of the relationship between the number of buds per polyp and time prior to the inflection point (Day 24 at 13°C, Day 21 at 16°C) is indicative of the rate of bud initiation. Following the inflection point the relationship plateaus as the rate of bud initiation reaches equilibrium with the rate at which buds became fully developed and were released as new daughter polyps (Figure 5.2). As such, the period of time from the

start of the experiment, when there were no buds, to the inflection point is indicative of the development time for buds from initiation to release. Additionally, the time at which treatments show an initial separation from each other is indicative of the time taken for colonies to begin responding to new conditions.

A comparison of the slope for each temperature shows that more buds are initiated at higher temperatures (Figure 5.2). New buds at 13°C were initiated at approximately twice the rate they were at 10°C while the rate at 16°C was approximately three times that at 10°C. The time taken for buds to develop from initiation to release was around 19-21 days at 16°C and around 24 days at 13°C. There is no evidence of an inflection point or a levelling of the relationship between time and the number of buds per polyp at 10°C suggesting that more buds were being initiated than daughter polyps released throughout the experimental period and that the development time of buds at that temperature was therefore longer than the 32 day experimental period.

Corresponding changes in the slopes of the relationship between average colony size and time (Figure 5.1) were evident around Day 19-21 at16°C and Day 24-26 at 13°C supporting the conclusion that a greater number of daughter polyps were being released from those days on. No change in the slope at 10°C is evident indicating a failure to reach equilibrium between bud initiation and bud development due to very slow bud development at this low temperature. The inferred development time for buds is only approximate because the population size at each treatment level was increasing prior to the inflection points identified,

although at lower rates. The number of developing buds was even in all temperatures during the first five days of the experiment. This is indicative of the rate of bud production for the conditions prior to the experiment (9°C and 33‰). Colonies held at 16°C responded after five days and colonies held at 13°C respond after 19 days. Colonies held at 10°C did not show any sign of a response to the change in temperature from the start of the experiment indicating a response time greater than 32 days at this temperature. However, the one-degree difference between the treatment temperature of 10°C and the conditioning temperature of 9°C prior to the experiment may not have been sufficient to elicit a response.

Temperature also had a significant effect on the number of buds present in colonies, relative to colony size, on the last day of the experiment ($F = 5.19$, df 2,17, $P = 0.017$), but salinity did not ($F = 1.98$, df 2,17, $P = 0.168$). There were almost twice as many buds in the 13°C and 16°C treatments than there were in the 10°C treatment while, again, there was no difference between the 13°C and 16°C treatments (Figure 5.3).

5.3.3 Number of actively budding scyphistomae

On the final day of the experiment there was no effect of temperature on the number of actively budding polyps ($F = 0.8$, df 2,17, $P = 0.464$), however salinity did have a significant effect ($F = 7.15$, df 2,17, $P = 0.006$). Approximately 40% more actively budding polyps were present in the 35‰ treatment (Figure 5.4). The seven percent difference between the 25‰ and 30‰ treatments was statistically significant,

however, such a small difference was not considered to be biologically important.

In contrast, temperature had a significant effect on the number of buds being produced by actively budding polyps on the last day of the experiment ($F = 7.09$, $df = 2,17$, $P = 0.006$), but salinity did not ($F = 0.11$, $df\ 2,17$, $P = 0.901$). There were approximately 60% more buds on polyps in the 13°C and 16°C treatments than there were in the 10°C treatment, while there was no difference between the 13°C and 16°C treatments (Figure 5.5).

5.3.4 Scyphistomae size

No significant differences in the size frequency distribution of polyps was found among the levels of temperature within each salinity, or among the levels of salinity within each temperature. There were significant differences between temperature treatments when salinity was pooled ($\alpha = 0.016$; $\chi^2 = 24.65$, $df\ 6$, $P < 0.001$), however salinity did not have an effect when temperature was pooled ($\alpha = 0.016$; $\chi^2 = 3.46$, $df\ 6$, $P = 0.747$). At the lowest temperature (10°C) there were 50% fewer small polyps (0.9-1.9mm) and 20% more large polyps (3.0-3.9mm and 4.0-4.9mm) than expected while at the highest temperature (16°C) there were 25% more small polyps (0.9-1.9mm) and 50% fewer large polyps (3.0-3.9mm and 4.0-4.9mm) than expected (Figure 5.6).

5.3.5 Mortality

The number of polyps dying or falling from experimental plates was not a function of temperature ($F = 1.3$, $df\ 12.6,113.3$, $P = 0.222$) or salinity

($F = 0.9$, df 12.6,113.6, $P = 0.549$). Mortality rates remained low throughout the experimental period at an average of 0.1 polyp per plate per day.

5.3.6 Iodine induction of strobilation

An additional attempt to induce strobilation was made following the 32 day experimental period using potassium iodide at a concentration of 10^{-4}M (Silverstone *et al.* 1977). Despite this, strobilation was not observed during a further 36 days during which time maintenance of scyphistomae in experimental temperature and salinity treatments continued. The experiment was not conducted at the time of year when strobilation would normally occur naturally, however, other researchers have readily been able to induced strobilation in scyphistomae of *A. aurita* within similar time frames to that of this experiment (e.g. Kakinuma 1975, Silverstone 1977, Keen and Gong 1989) and it is not known why strobilation did not occur in this study.

5.4 Discussion

The potential for a bloom of *Aurelia* sp. medusae, in the form of number of ephyrae liberated, in any given year in south east Tasmania is directly related to the size of the benthic scyphistomae population at the time of strobilation (Brewer and Feingold 1991, Watanabe and Ishii 2001, Colin and Kremer 2002), the proportion of those scyphistomae strobilating, and the number of ephyrae produced per individual scyphistomae. This study set out to examine how different temperature

and salinity regimes affected the population dynamics of the scyphistomae of *Aurelia* sp. The results show both temperature and salinity can significantly affect the pattern of allocation of energy resources between growth and reproduction within the scyphistomae (Table 5.2). This will have ramifications for the distribution, abundance, and survival of the scyphistomae (Garrabou 1999) and may in turn have a large effect on the distribution and abundance of medusae in the following summer (Lucas 2001). The results presented here provide important information for further understanding the reproductive biology and life history strategy of *Aurelia* spp. in general and in particular for *Aurelia* sp. in Tasmania.

Population growth rates of *Aurelia* sp. colonies increased with temperature. These results show that higher growth rates at higher temperatures were the result of more buds developing per scyphistomae along with faster development and earlier release of daughter scyphistoma to the substrate. *Aurelia aurita* also shows a similar response to temperature (e.g. Kakinuma 1975, Omori *et al.* 1995, Kroiher *et al.* 2000), although the biological mechanisms responsible were not determined. In contrast, bud production in *Chrysaora quinquecirrha* is not affected by temperature (Purcell *et al.* 1999b). There was also some evidence in the results to suggest that the time taken to start responding, by modifying the rate at which new buds are initiated, is also temperature dependent. The time frames involved suggest that any increases in rates of colony growth will only occur when temperature changes are at a scale of weeks or greater.

Although population growth was not statistically significant in the 10°C treatment, there was a numeric increase in all replicate colonies at that temperature indicating that asexual reproduction was taking place albeit at a reduced level. Additionally, mortality rates were not different among temperature treatments. Budding in *A. aurita* stopped altogether when temperatures were reduced to 5-8°C (Kakinuma 1975), and disintegration of the scyphistomae occurred when temperatures were lowered to 4°C (Kroiher *et al.* 2000). Naturally occurring scyphistomae colonies are unlikely to experience prolonged periods with temperatures lower than 10°C in south east Tasmania (CSIRO 2000), therefore temperature alone was not expected to explain any population decline observed in this natural environment. However, asexual bud production may be suppressed to nearly zero during the coldest part of the year.

Salinity had no effect on the growth of colonies within the range tested. This finding is in keeping with Watanabe and Ishii (2001) who report successful asexual reproduction in the scyphistomae of *A. aurita* in Japanese waters in salinities as low as 0.1‰. On the other hand, the increase in the geographical range of *A. aurita* in Finland has been attributed to a rise in salinity levels creating more suitable conditions for reproduction (Palmen 1953), although it was not clear which part of the life cycle was being inhibited by the lower salinities previously encountered. Similarly, mortality rates were not affected by salinity. *A. aurita* scyphistomae are also very tolerant to a range of salinities in experiments, where they survive salinities ranging from freshwater through to twice that of their normal environment (Halisch 1933). The

salinity range tested in this study corresponded to salinity conditions likely to be encountered by naturally occurring colonies in south east Tasmania (CSIRO 2000). The tolerance of the scyphistomae stage to a wide range of salinity regimes allows colonies to survive and continue to grow in order to maximise production of the pelagic ephyrae in the characteristically unstable estuarine environment. The proportion of scyphistomae that were actively producing buds was dependant on salinity with more active scyphistomae at the highest salinity than at lower salinities. Interestingly this relationship had no detectable effect on colony growth and hence a salinity effect would not have been identified if colony dynamics were only examined at the whole colony level.

Exponential numeric growth of colonies was observed at higher temperatures. This type of growth of colonial organisms is typically seen in the absence of any density dependant factors (Stearns 1992, Gong 2001), particularly resource limiting factors such as food, space, and nutrients. A break down of exponential growth of *A. aurita* scyphistomae in experimental conditions occurs after 15 days as scyphistomae density increases (Coyne 1973). The resulting sigmoidal growth pattern was attributed at least partially to "some soluble factor produced by the scyphistomae themselves and released into the medium" which acted by retarding bud initiation rates. This type of growth was not observed in our experiments with the highest absolute growth rates being recorded in the last three days of the experiment in all temperature treatments. The assumption was made that naturally occurring colonies of *Aurelia* sp are

similarly unlikely to be subject to such an increase in concentrations of this soluble factor. Space might have become limiting had the experiment run for longer resulting in the appearance of sigmoidal type growth curves. Other physiochemical factors that may have influenced colony growth and reproduction such as irradiance levels, food availability, and water quality were controlled in the experiment and as such are not thought to have contributed to the differences observed between treatments.

Growth rates of colonies are ultimately driven by responses of individual scyphistomae. The effect of temperature, seen repeatedly at the level of the colony, was repeated at the level of individual scyphistomae in the number of buds present on active scyphistomae and the number of buds in colonies. The rate at which individual scyphistomae initiate new buds, the number of developing buds on scyphistomae and the rate of development of these buds are all important for determining colony growth.

The size of scyphistomae at the end of the experimental period was affected by temperature but not by salinity. Scyphistomae were shunting energy resources toward bud production when conditions were warm, resulting in high population growth rates and smaller individuals, and towards somatic growth when conditions were cooler, resulting in low population growth rates and larger individuals. Many populations of *A. aurita* only begin to strobilate after a critical winter minimum is reached (Omori *et al.* 1995, Kroiher *et al.* 2000). Scyphistomae increased in size and produced the fewest buds in the 10°C treatment. This temperature

was approximately equivalent to the winter minimum temperature experienced by the scyphistomae of *Aurelia* sp. in south east Tasmania during the time preceding the onset of strobilation. Larger scyphistomae produced more ephyrae (Spangenberg 1964b, Gong 2001) and budding and strobilation are mutually exclusive (Gong 2001) so scyphistomae that increased in size and had low budding rates may in fact have been preparing for strobilation in the 10°C treatment.

Critical low winter water temperatures, abundant food supply and irradiance levels are important in the initiation of strobilation in *A. aurita* scyphistomae. Strobilation was not observed in the experimental period, despite the scyphistomae going through a "conditioning" period with low temperature (8-9°C) (e.g. Kroiher *et al.* 2000), and low light conditions prior to the experiment. Clonal theory suggests that the release of dispersive rametes will be favoured in hard times (Stearns 1992). The lack of a strobilating response in the experiment may indicate that the experimental treatment levels were not "stressful" to the scyphistomae. This seems plausible considering the experimental temperature and salinity conditions scyphistomae were exposed to were based on those likely to be experienced in the Tasmanian environment during a typical annual cycle, in addition to the fact that they were fed to satiation. The low density of scyphistomae within the replicate colonies may have played a role in the failure of strobilation (Silverstone *et al.* 1997, Keen 1991), however, spontaneous strobilation in low density cultures can occur (Gong 2001).

The results of this experiment suggest that scyphistomae populations will grow rapidly over summer with growth continuing into autumn, although at a reduced rate, resulting in high numbers of scyphistomae by winter. During the coldest part of winter budding activity will have slowed and scyphistomae will be increasing in size leading up to strobilation at the end of winter. Since larger scyphistomae are able to produce more ephyrae (Spangenberg 1964b, Gong 2001) this strategy would result in more ephyrae being released during strobilation at the end of winter in south east Tasmania (pers. obs.). Additionally, the timing of strobilation is such that ephyrae are able to take advantage of an expected spring bloom (Cheshuck 2001). Following strobilation, scyphistomae in natural colonies would experience warming water temperatures and an abundant food supply suited to faster colony growth rates in addition to rebuilding tissue lost during strobilation (Miyake *et al.* 2002).

Maintenance of a large population of healthy scyphistomae in south east Tasmania enables *Aurelia* sp. populations to maximize 'bloom potential', in the form of large numbers of ephyrae released into the water column, every year. This study has shown that scyphistomae colonies are able to survive a wide range of temperature and salinity conditions. The results suggest populations of scyphistomae in the wild would increase year-round with the fastest growth rates in summer and the slowest growth rates in winter, although other factors including competition for space (Colin and Kremer 2002, Watanabe and Ishii 2002), competition for food (Harper 1985), food availability (Hernroth and Grondahl 1985a,

Purcell *et al.* 1999b), and predation (Keen 1991, Osman and Whitlatch 2004) can also play a role in determining the growth and survival of scyphistomae populations. The ability of wild scyphistomae populations to reliably grow and survive through a broad range of conditions spanning many seasons is vital for the survival of scyphozoan populations where successful cycling of the full life cycle may not occur for several years.

Table 5.1 A summary of factors linked with modifying asexual reproduction in scyphistomae.

Modifying Factor	Species	Author(s)
Light	*Aurelia aurita*	Custance (1964)
Temperature	*Aurelia aurita* *Chrysaora quinquecirrha*	Spangenberg (1968), Coyne (1973), Kakinuma (1975), Omori *et al.* (1995), Kroiher *et al.* (2000), Miyake *et al.* (2002), Purcell *et al.* (1999b)
Salinity	*Chrysaora quinquecirrha*	Purcell *et al.* (1999b)
Food availability	*Aurelia aurita* *Chrysaora quinquecirrha*	Spangenberg (1964b), Keen and Gong (1989), Keen (1991), Gong (2001), Bamstedt *et al.* (2001), Purcell *et al.* (1999b)
The concentrations of chemicals and compounds	*Aurelia aurita*	Spangenberg (1967, 1968), Silverstone *et al.* (1977)
The presence of zooxanthellae	*Cephea cephea*	Sugiura (1966)
Predator density	*Aurelia aurita* *Cyanea capilata*	Hernroth and Gröndahl (1985a, b), Gröndahl (1988b), Keen (1991) , Gröndahl and Hernroth (1987)

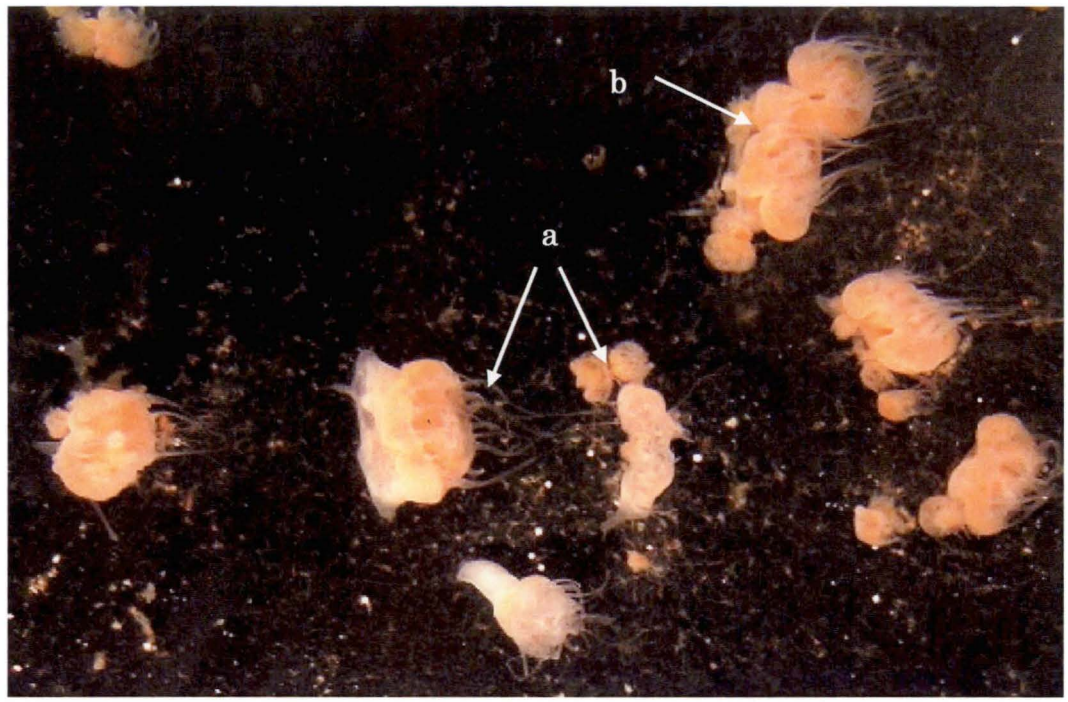

Plate 5.1 Photograph showing *Aurelia* sp. scyphistomae colony on experimental plates with: (a) scyphistoma, and (b) attached bud. The larger individuals are the wild caught scyphistomae transplanted to form the experimental colony. The smaller individuals are daughter scyphistoma which have developed during the experiment.

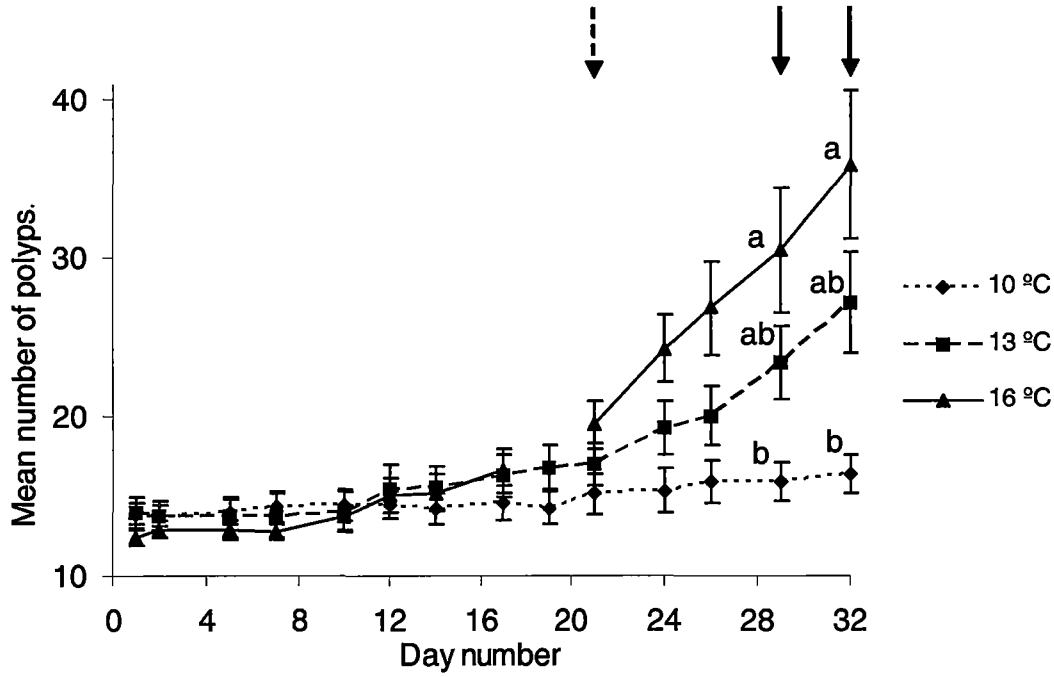

Figure 5.1 Mean number (±se) of polyps through time. Solid arrows indicate days when significant differences were found among the three temperatures (n = 9). The dashed arrow indicates the day (Day 21) when the number of polyps held at 13°C and 16°C had increased significantly from the start of the experiment. Letters indicate which means are similar as determined by Tukey's HSD post-hoc test. Salinity has been pooled for graphing.

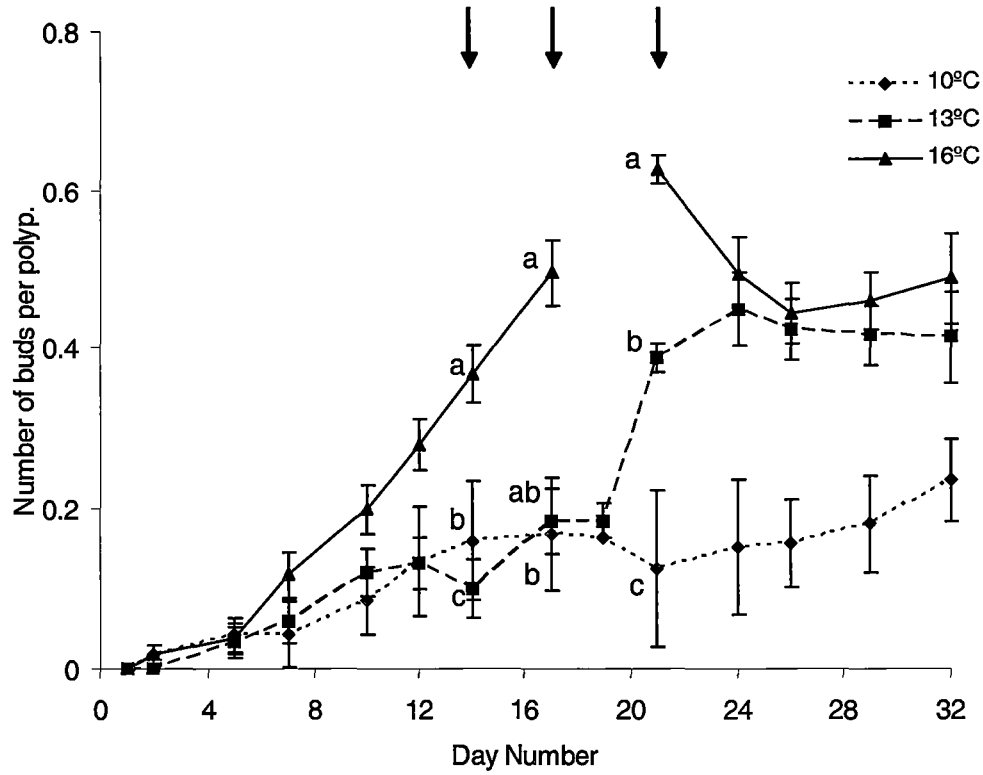

Figure 5.2 The number of buds per colony (±se) adjusted for he number of polyps in the colony (n = 9). The arrows indicate days when a significant difference was detected among the temperatures. Letters indicate which adjusted means are similar as determined by modified *t*-tests (Quinn and Keough, 2002).

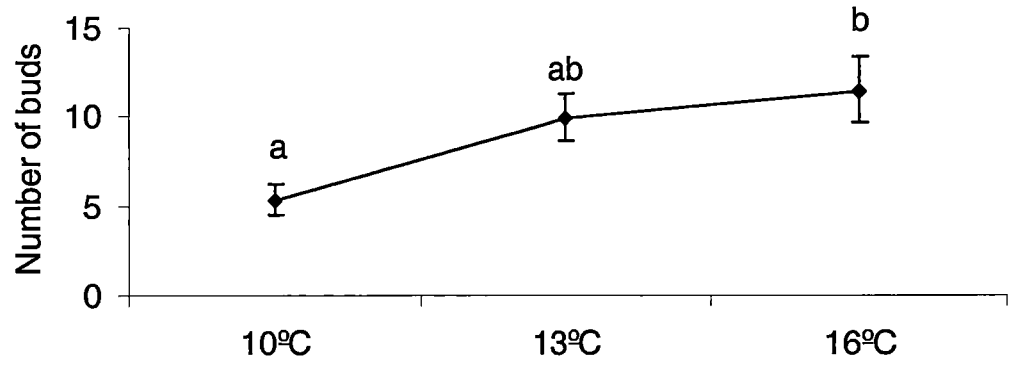

Figure 5.3 The mean number of buds (±se) present in colonies in each temperature treatment on Day 32 adjusted for the number of polyps in the colony (n = 9). Means with different letters are significantly different from one another. Note that means and se's are back-transformed.

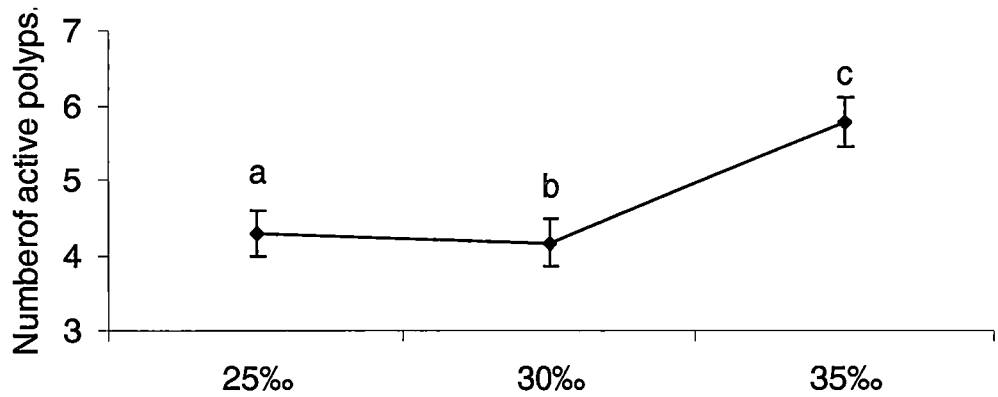

Figure 5.4 The mean number (±se) of polyps actively budding in each salinity treatment on Day 32, adjusted for the number of polyps in the colony (n = 9). Means with different letters are significantly different from one another.

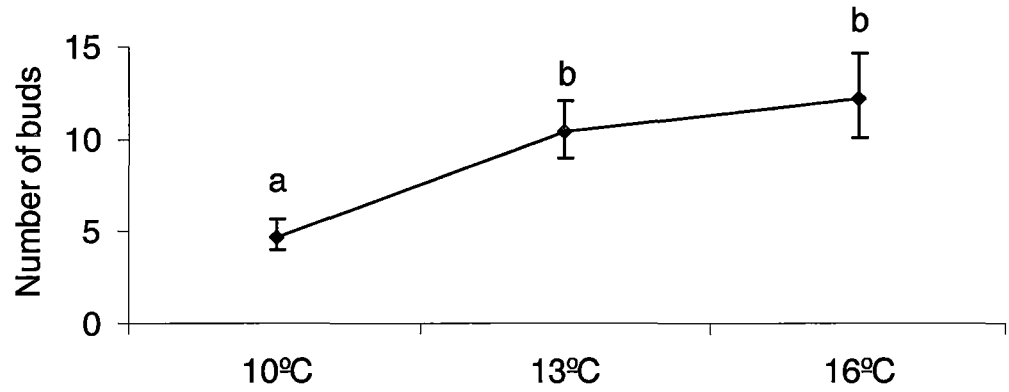

Figure 5.5 The mean number of buds (±se) present on actively budding polyps in each temperature treatment on Day 32 adjusted for the number of actively budding polyps in the colony (n = 9). Means with different letters are significantly different from one another. Note that means and se's are back-transformed.

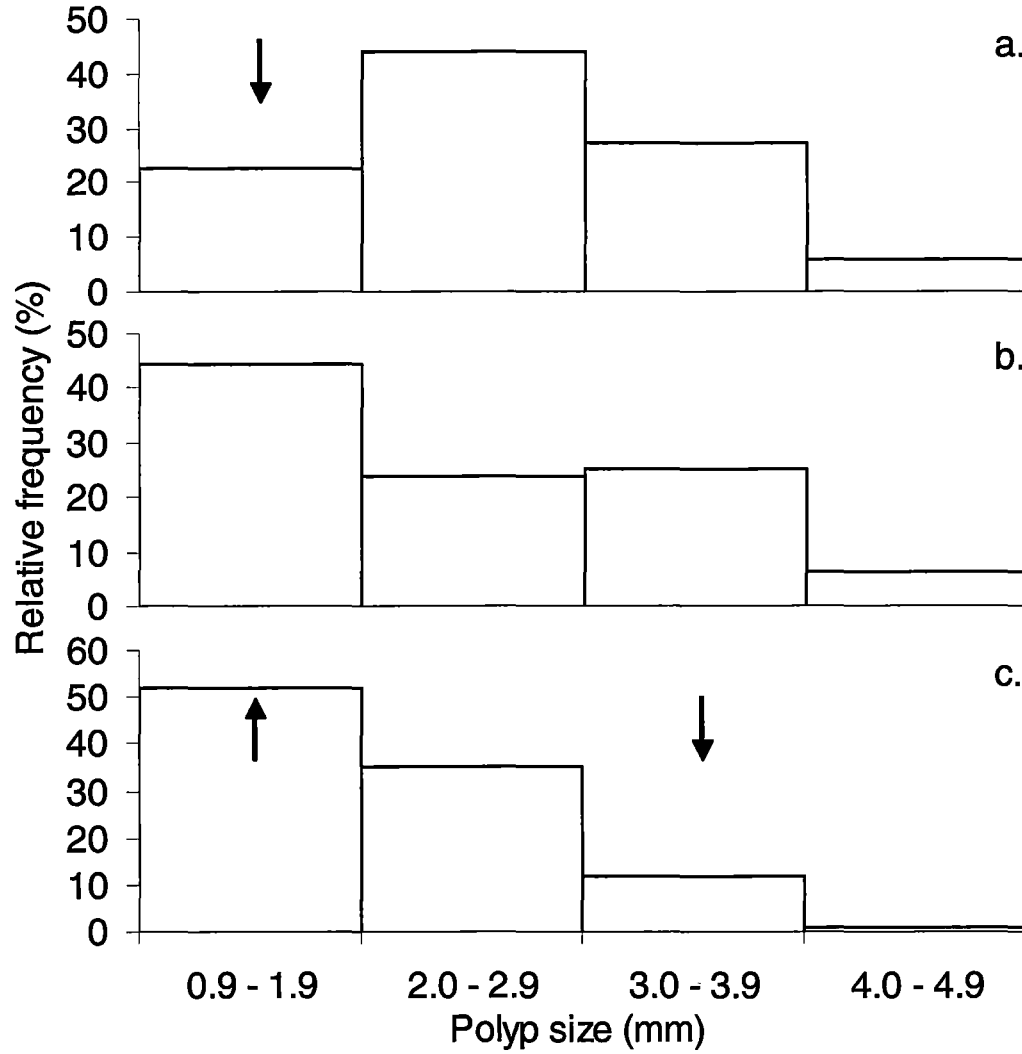

Figure 5.6 The size frequency distribution of polyps on Day 32 in three temperature treatments; a) 10°C, b) 13°C, and c) 16°C. Arrows indicate where and in which direction the observed results were different than expected.

Table 5.2 Summary of the responses of *Aurelia* sp. scyphistomae to temperature and salinity. Arrows indicate the direction of change in the population variable in response to an increase in the environmental factor (temperature or salinity). A dash indicates no change or effect was found.

Response Variable	Environmental Variable	
	Temperature	Salinity
Colony growth	↑	—
Number of buds in a colony	↑	—
Number of actively budding scyphistomae	—	↑
Number of buds per active scyphistomae	↑	—
Scyphistomae size	↓	—
Mortality	—	—

CHAPTER 6:

GENERAL DISCUSSION

6.1 SYNTHESIS

The central thesis of this research was to determine the mechanisms involved in the development of blooms of *Aurelia* sp. medusae in south east Tasmania, and to better understand how the life history strategy of scyphozoans enables them to succeed in a diverse range of environmental conditions. This study examined patterns in the life history of both the pelagic and benthic stages of the life cycle (Figure 6.1) and developed hypotheses as to how the life cycle of *Aurelia* sp. functions and which part or parts of the life cycle are potentially critical to the occurrence of medusae blooms in south east Tasmania. The approach of this study can be summarised in four main parts:

1) An assessment of evidence linking environmental factors to the presence or absence of medusae in any summer;
2) A comprehensive description of the growth and development of the medusa phase *in situ* in the Huon Estuary in south east Tasmania;
3) An assessment of the role of individual medusae behaviour in aggregation formation and maintenance; and
4) An assessment of the spatial and temporal patterns of population dynamics of the scyphistomae in the wild and the laboratory.

The results presented in Chapter 2 show that salinity, rainfall, and Southern Oscillation Index (SOI) values through autumn, winter, and spring were related to the occurrence of blooms of *Aurelia* sp in summer (Figure 6.1). Similar links between environmental conditions and the abundance and distribution of marine organisms are common, however it

is widely acknowledged that these environmental factors are not always operating directly on the life history stages of these animals (e.g. Harris *et al.* 1988, Lucas and Lawes 1998, Lynam *et al.* 2004), but rather indirectly through other unmeasured local physical or biological parameters such as food availability (e.g. Hernroth and Gröndahl 1983, 1985a, Keen and Gong 1989, Purcell *et al.* 1999b), nutrients (Chen *et al.* 1985), and predator abundance (e.g. Gröndahl 1988b, Keen 1991).

Large spatial and temporal differences in the population dynamics of scyphistomae (i.e. the number of scyphistomae, the rate of colony growth through budding, and the amount of strobilation) were found in this study. The abundance and distribution of the scyphistomae is considered to be of critical importance to the distribution and abundance of the bloom forming medusae stage (Brewer and Feingold 1991, Lucas 2001, Mills 2001, Watanabe and Ishii 2001, Colin and Kremer 2002). Therefore, factors contributing to variability of the life history characters of the scyphistomae (Figure 6.1) are likely to be important in determining the number of ephyrae released into the water column, and therefore the potential number of medusae. Additionally, predators such as nudibranchs and gastropods can have a large impact on scyphistomae distribution and abundance (e.g. Gröndahl 1988b, Keen 1991). However, evidence of scyphistomae population declines through predation, or the presence of large populations of such potential predators were not observed during monitoring of colonies in south east Tasmania.

Regular monitoring of scyphistomae colonies found evidence of strobilation occurring in each of the three years during this project. The

subsequent failure of medusae blooms to develop in two of those years suggests a failure in the recruitment of ephyrae to the medusae stage in those years (Figure 6.1). This agrees with the suggestion that mortality during the ephyrae stage is important in determining medusae abundance (Purcell *et al.* 1999b). However, it is contrary to the belief that mortality of ephyrae and juvenile medusae is low (Schneider 1989). The results of this study suggest that mechanisms, such as food availability (Hernroth and Gröndahl 1983, Sullivan *et al.* 1997, Båmstedt *et al.* 2001), affecting mortality of the ephyrae override the importance of mechanisms involved in the distribution, abundance, and ephyrae production of the scyphistomae in determining the coarse presence/absence pattern of medusae (blooms) in south east Tasmania.

6.2 LIFE HISTORY THEORY

The complex and unique life history adopted by many scyphozoans potentially delivers them great dividends in terms of ecological fitness. Asexual and sexual reproduction in benthic invertebrates such as corals (e.g. Harrison and Wallace 1990, Brazeau and Lasker 1992) and echinoderms (e.g. Sköld *et al.* 2002) is common (Hughes 1989), but the occurrence of reproduction in two separate stages of the life cycle is unusual. Both parts of the life cycle of scyphozoans possess powerful mechanisms for increasing population size in their own right, and each part has unique advantages not enjoyed by the other.

The scyphistomae can grow free from morphological and physiological restraints faced by aclonal organisms such as maximum

size, senescence, and surface area to volume ratios. They also have some of the advantages of larger animals such as greater food capture ability and protection from predation, as well as some of the advantages of smaller animals, such as not being limited by spaces where they can physically fit (Hughes and Cancino 1985, Marfenin 1997, Gong 2001). Clonality and modular growth in sessile organisms also promotes local exploitation of resources and spreads the risk of genet mortality (Karlson *et al.* 1996). Also, an investment in colony growth now also represents an investment in the production of sexual propagules in the future (Jackson 1985). Advantages of the medusae form include: the ability to utilize available food resources to grow extremely rapidly, thus increase fecundity (e.g. Matsakis and Conover 1991, Lucas and Lawes 1998), and dispersal advantages (e.g. Williams 1975, Harrison and Wallace 1990). These features may give scyphozoans an advantage over other organisms, and explain their dominant position in many marine ecosystems (e.g. Schneider and Behrends 1994, Gilabert 2001, Brodeur *et al.* 2002).

The success of a population in a changeable physical and biological environment, such as the estuarine environment of south east Tasmania (CSIRO 2000, Green and Coughanowr 2003), depends on having phenotypic plasticity of its life history characteristics (Warner 1991, Roff 1992). Both stages of the life cycle of scyphozoans exhibit high levels of plasticity in their responses to environmental conditions (e.g. Medusa: Lucas and Williams 1994, Ishii and Båmstedt 1998, Lucas and Lawes 1998; Scyphistoma: Olesen *et al.* 1994, Purcell *et al.* 1999b, Gong 2001). The occurrence of an *Aurelia* sp. medusae bloom in only one year and in

one region during the study did not allow for comparisons of the responses of the medusae to be made, however the scyphistomae showed high levels of plasticity in their responses to both natural and experimental environmental variation.

The resilience of the perennial benthic scyphistomae appears to be the stronghold for survival of the population, providing a refuge against the year-to-year 'success or failure' nature of the short-lived pelagic medusae stage. This resilience of one phase of the life cycle is successfully used against population extinction in other bloom forming organisms such as dinoflagellates with dormant cysts (e.g. Doblin *et al.* 1999, Figueroa and Bravo 2005), insects with a diapause phase such as locusts (e.g. Tanaka and Zhu 2003, Nahrung and Allen 2004), and many flowering plants with dormant seeds. However, in these examples, resumption of the life cycle is often dependent on the arrival of favourable environmental conditions, where the scyphistomae of *Aurelia* sp. appear to have the capacity to strobilate each year.

The commencement of strobilation, despite the prospect of unfavourable conditions, seems a potential waste of reproductive effort. However, there was some variability in characters involved in determining the number of ephyrae produced (proportion of scyphistomae population strobilating and duration of strobilation) suggesting scyphistomae may respond to unfavourable conditions by moderating the effort expended on the sexual phase and investing in colony growth and maintenance instead (e.g. Williams 1975, Hughes 1989). The pattern of reproducing every year, despite the conditions, is one that has been

successfully adopted by many marine broadcast spawners. Such reproductive strategies represent a trade-off of few, well developed and expensive offspring with high probability of survival (k-strategists) in favour of lots of low cost offspring with low probability of survival (r-strategists) (Roff 1992, Stearns 1992). This type of strategy can result in years of poor recruitment due to unfavourable conditions, but conversely, can also result in years where recruitment is very high (e.g. broadcast spawning fish, Hollowed *et al.* 2001). *Aurelia* medusae are dioecious and therefore must be in close proximity to members of the opposite sex for fertilisation to occur (Arai 1997). This component of the reproductive strategy of *Aurelia* may be necessary to achieve sufficient densities of medusae in the environment to facilitate successful sexual reproduction. Sexual reproduction is important, despite the cost, because it contributes toward the genetic variation of life history characters evident in the scyphistomae (Keen and Gong 1989, Keen 1991, Gong 2001) that permit natural selection to drive organisms toward increasing fitness and the optimal combination of life history traits (Roff 1992). Without periodic introduction of genotypic variability through successful functioning of the life cycle and sexual reproduction in the medusae, natural selection may drive individual colonies toward more limited variability and increased susceptibility to change.

6.3 APPLIED SIGNIFICANCE

This project has provided a great deal of valuable information about the functioning of the life cycle of *Aurelia* sp. and the mechanisms leading

to blooms of medusae, and has addressed some of the major concerns held by the Atlantic salmon aquaculture industry in southern Tasmania. One of the most valuable components of the project has been the development of a relatively simple-to-use model that calculates the probability of medusae blooms developing. The inputs for the model are environmental data that have been, and will continue to be collected routinely, and are easily accessible. Mean winter salinity less than 34.5ppt, total autumn rainfall lower than 100mm, and positive southern oscillation index values for winter and spring were all linked with the occurrence of medusae blooms in the following summer. A limitation of the model in its current form is that it is based on a very short time series of data (eight years) due to the lack of information concerning bloom occurrence in the region prior to 1997. Management can easily make improvements to the robustness of the model with the addition of each additional year of information in the future.

Aquaculture companies held a general concern that aggregations of *Aurelia* sp. medusae were targeting lease sites and caged Atlantic salmon. The assessment of aggregation dynamics made in this study suggests this is not the case. Aggregations of scyphozoans have been observed purposely moving in a given direction (e.g. Hamner *et al.* 1994, Schuyler and Sullivan 1997, Dawson and Hamner 2003), however aggregations in the Huon Estuary were observed to drift predominantly with the local current patterns in the area. The conclusion of this study is that aggregations of medusae encounter lease sites incidentally as a result of tidal flushing of the estuary. Therefore, short term removal of

sea cages out of the path of these transient aggregations may be a viable management option.

The identification of scyphistomae colonies on aquaculture farm structures has been an important discovery. Man made structures provide an ideal habitat for the scyphistomae and the increased amount of structure (Graham *et al.* 2001, Miyake *et al.* 2002), including farm structures, in the waterways of south east Tasmania in the last decade may have contributed to the increased prominence of blooms during this period. Medusae populations are often found in close association with the scyphistomae population (Lucas 2001, Colin and Kramer 2002), therefore the large colonies found at some aquaculture sites may be directly contributing to blooms of medusae causing problems in those areas. As such, a management plan for minimising the risk of financial loss through stock damage and mortality could include the monitoring of farm structures to detect the establishment and growth of scyphistomae colonies. Evidence of strobilation has been observed in south east Tasmania in August each year. A management strategy to reduce the amount of ephyrae produced each year would be most effective if the number of scyphistomae were reduced close to, but before this time, giving colonies little time to rebuild prior to the strobilation period.

'Bloom potential' in the form of the number of ephyrae liberated is directly related to the size of the benthic scyphistomae population at the time of strobilation (Brewer and Feingold 1991, Watanabe and Ishii 2001, Colin and Kremer 2002), the proportion of those scyphistomae strobilating, and the number of ephyrae produced per individual

scyphistomae. The size of colonies of *Aurelia* sp. scyphistomae, and therefore their population size, was ultimately physically restricted by the total available area of their preferred habitat (flat undersurfaces of hard substrates). Already mentioned above is the fact that various aquaculture farm structures provide ideal habitat for scyphistomae colonies and it is thought that the proliferation of such structures in the marine and estuarine environments associated with an expanding aquaculture industry may be contributing significantly to the 'bloom potential in any year (Miyake *et al.* 2002).

The rate of budding, the density of scyphistomae and the degree of strobilation varied with colony location and among years. Some colony locations were clearly more suited to scyphistomae productivity than others with sites within the D'Entrecasteax Channel having the greatest bloom potential per unit area of suitable habitat. It is recommended that relevant aquaculture structures within this region be regularly examined for the presence of scyphistomae colonies and steps be taken to remove or reduce these populations periodically. Temperature, rainfall and competition for space from other benthic species were also linked with scyphistomae density. These results of this project suggest that warmer years and warmer periods within years will produce accelerated colony growth relative to those cooler years and periods with ambient water temperatures less than 10 °C resulting population decline. Mean daily rainfall was inversely correlated with scyphistomae density, with wetter periods resulting in a reduction in bloom potential. This finding ties in

well with the relationship between wetter autumns and the absence of medusae blooms in those years.

6.4 FUTURE RESEARCH

Obviously numerous other inter-connecting biotic and abiotic processes not examined in this thesis may contribute to the development of blooms of *Aurelia* sp. medusae in south east Tasmania. The results of this thesis have provided significant insight into the functioning of the life cycle, and have highlighted several key areas where further investigation is required in order to better understand the processes leading to blooms.

Tracking movement of newly strobilated ephyrae through to their appearance as juvenile medusae in aggregations is essential to predicting the intensity and location of blooms. Blooms of medusae appear suddenly in south east Tasmanian waters up to two months following strobilation, however no information linking *Aurelia* sp. medusae blooms to 'source' colonies was gleaned in this study. A genetic study of known colonies and medusae in discreet aggregations throughout south east Tasmania would provide valuable information for determining if all medusae within an aggregation came from one scyphistomae colony, if blooms originate from locally occurring scyphistomae colonies, and if scyphistomae and medusae form discreet populations within different regions of south east Tasmania.

Critical future work to determine where ephyrae go and what happens to them between strobilation and their appearance as juvenile

medusae in aggregations needs to be conducted. Results presented in this thesis indicate that recruitment failure of the ephyrae stage may be a powerful moderator of medusae density. In light of this, the lack of knowledge of the habits of the ephyrae of *Aurelia* sp., and the mechanisms involved in their development and recruitment stand out as an important direction for future research. Determining the response of ephyrae to basic biotic and abiotic factors such as temperature, salinity and food availability can readily be achieved in aquaria (e.g. Sullivan *et al.* 1997, Båmstedt *et al.* 2001) and would provide valuable data for comparison with environmental conditions in the field. A study of the patterns of distribution and development of ephyrae in the field is also needed. Sampling with plankton nets throughout the region failed to capture any *Aurelia* sp. ephyrae during this study. Nevertheless, this type of sampling has proven to be successful in studies of ephyrae distribution and development (e.g. Hernroth and Gröndahl 1983, 1985a, Gröndahl and Hernroth 1987) and could be successful in south east Tasmania with a more targeted approach utilising the knowledge of colony locations and strobilation periods gained in this study.

Further work is required to gain a better understanding of the factors involved in the timing and rate of strobilation. The current project examined population dynamics of scyphistomae in the laboratory and in the field. However, the failure of strobilation to occur in the laboratory experiments, and the nature of the field monitoring meant the data collected was primarily limited to processes involved in budding and colony growth. Much research has been done on the effects of

environmental factors on the timing of strobilation and the production of ephyrae (e.g. Hernroth and Gröndahl 1983, Gröndahl and Hernroth 1987, Purcell *et al.* 1999b, Watanabe and Ishii 2001, Miyake *et al.* 2002). Determining how environmental factors influence the proportion of scyphistomae strobilating, and the number of ephyrae produced per strobila is necessary for estimating the number of ephyrae released into the environment, and represents a clear gap in the current understanding of the processes involved in the development of blooms.

Further study of the mechanisms involved in the concentration of large numbers of *Aurelia* sp. medusae in south east Tasmania is clearly needed to answer the many questions generated by this study. A distinctive feature of the *Aurelia* sp. medusae population in south east Tasmania is the formation of incredibly dense and discrete aggregations. The findings of this study indicated that maintenance of these aggregations was facilitated by swimming behaviour of individuals, and further, that complex patterns of coordinated swimming evident within aggregations may also be important in maintaining aggregation integrity in the high-current environment of the Huon Estuary. The formation of aggregations is generally thought to be the result of passive or active responses to physical environmental conditions (e.g. Mackie *et al.* 1981, Hamner *et al.* 1982, Hamner and Shneider, 1986, Mutlu 2001). Behavioural studies using SCUBA diver observation and underwater video have been successfully used previously (Miyake *et al.* 1997, Toyokawa *et al.* 1997, Purcell *et al.* 2000, Dawson and Hamner 2003), as well as in this study. Aquarium based studies have also been of some use

(Mackie *et al.* 1981, Schuyler and Sullivan 1997) however the confinement of aggregating organisms in tanks is generally considered to disrupt behavioural patterns. This study was unable to associate any physical properties of the water column with the location or boundaries of aggregations. The idea that aggregations may be self perpetuating is novel in scyphozoans. As aggregations were only found in one summer of this three year project, only a brief glimpse of this important and fascinating aspect of the medusae biology was possible during the course of this project.

The complex nature of the life cycle of scyphozoans makes unravelling the factors and processes involved in the development of medusae blooms extremely difficult. Consequently, the current level of understanding of scyphozoan biology and their life history strategies is still poor. The results of this study considerably broaden the picture as to factors involved in the formation of medusae blooms, and techniques developed in this thesis provide a platform for future studies. Investigations of the nature outlined above will make advances towards resolving the many unanswered questions in relation to the variation and inherent flexibility in the life histories of scyphozoans.

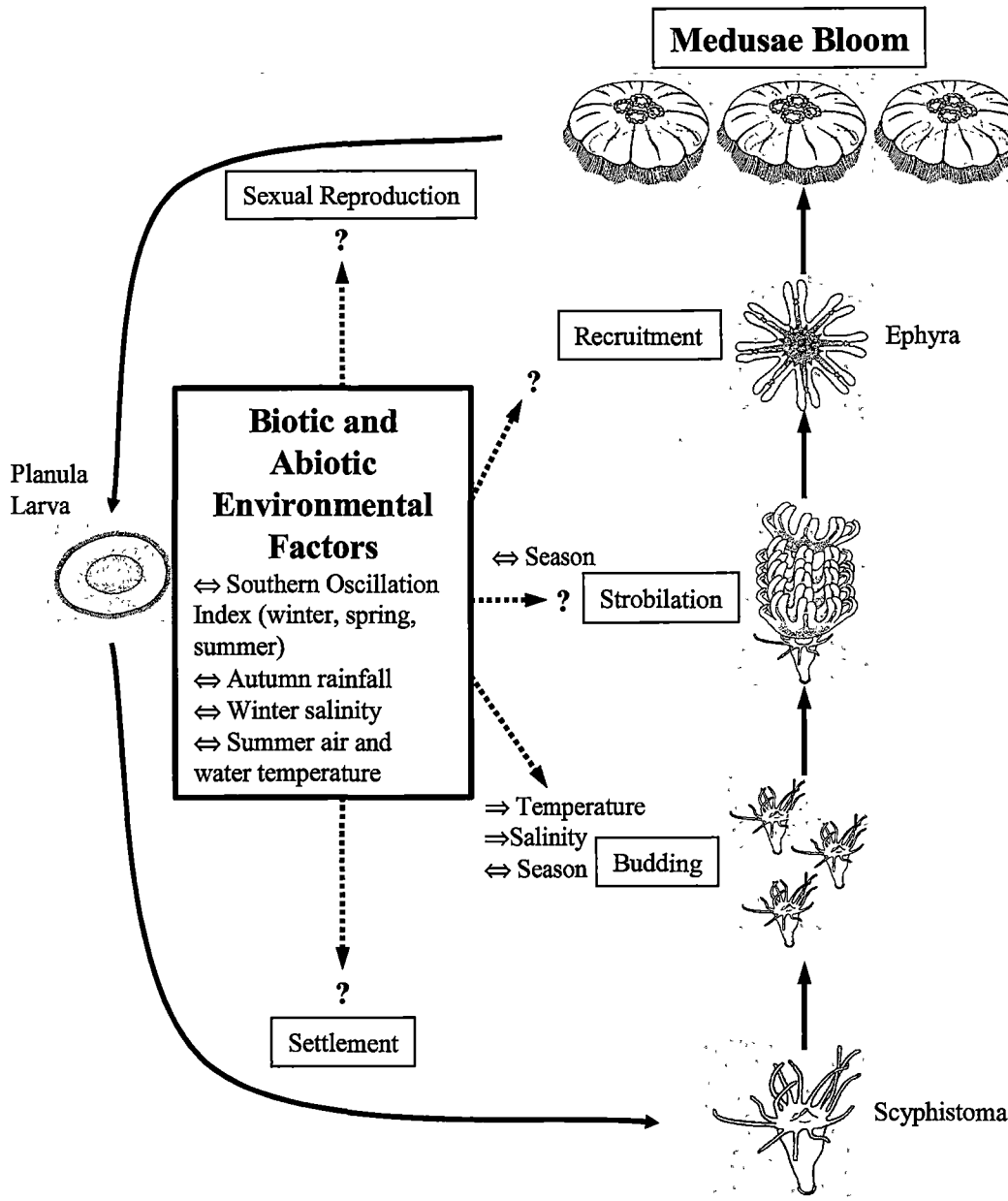

Figure 6.1 Summary of the common life cycle of *Aurelia* spp. indicating the biotic and abiotic environmental factors this project has implicated in influencing the formation of blooms of *Aurelia* sp. medusae in south east Tasmania. (⇒) Signifies a direct link to life history character plasticity, (⇔) signifies an indirect link to medusae bloom formation.

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